

Copepoda (Siphonostomatoida: Dirivultidae) from Hydrothermal Vent Fields on the Central Indian Ridge, Indian Ocean

JIMIN LEE¹, DONGSUNG KIM¹ & IL-HOI KIM^{2,3}

¹Marine Ecosystem Research Center, Korea Institute of Ocean Science & Technology, Busan 49111, Korea. E-mail: leejm@kiost.ac.kr, dskim@kiost.ac.kr

²Korea Institute of Coastal Ecology, Bucheon 14449, Korea. E-mail: ihkim@gwnu.ac.kr

³Corresponding author

Abstract

Eight species of copepods belonging to the family Dirivultidae (Siphonostomatoida) are described from deep-water hydrothermal vent fields on the Central Indian Ridge in the Indian Ocean. *Aphotopontius limatulus* Humes, 1987, previously known only from the East Pacific, is included. The other seven species are new, as follows: *Aphotopontius kiost* n. sp., *A. muricatus* n. sp., *Benthoxynus constrictus* n. sp., *Stygiopontius spinifer* n. sp., *S. horridus* n. sp., *S. geminus* n. sp., and *S. quadripaxillifer* n. sp. The copepodid I stage of *S. horridus* n. sp. is also described. This is the first record on copepods living on hydrothermal vent fields in the Indian Ocean.

Key words: *Aphotopontius*, *Benthoxynus*, *Stygiopontius*, new species, Onnuri Vent Field

Introduction

Deep-sea hydrothermal vents are scattered world-wide along the global midocean ridge system, with communities composed of specialized animals, dependent on chemoautotrophic microorganisms that exploit the reduced compounds abundant in vent fluids (Teixeira *et al.* 2011). Since the discovery of hydrothermal vents in the late 1970s, more than 250 active vent fields have been confirmed worldwide, and more than 400 new animal species have been described from these environments (Copley *et al.* 2016). The invertebrate fauna from the Indian Ocean hydrothermal vent was first discovered by Hashimoto *et al.* (2001) at the Kairei vent field. Subsequently, Van Dover *et al.* (2001), Nakamura *et al.* (2012) and Copley *et al.* (2016) reported fauna from the Edmond, Dodo, and Longqi vent fields, respectively, with three to 34 animal species identified in each of these vent fields.

Hydrothermal vent fauna include most animal phyla, but the most conspicuous and well-known are polychaetes, mollusks and crustaceans (Schander *et al.* 2010). Copepods contribute more than 15% of all known animal species reported from hydrothermal vents worldwide (Tunnicliffe *et al.* 1998), but no copepod has been hitherto recorded from Indian Ocean vent fields. The Dirivultidae, a copepod family of the order Siphonostomatoida, is the most diverse animal family found in vents (Gollner *et al.* 2010), with 13 genera including 53 described species.

In July and August 2017 and June 2018, the Korea Institute of Ocean Science and Technology (KIOST) conducted expeditions using the research vessel RV *ISABU* to explore hydrothermal vent fields on the Central Indian Ridge, and dredged benthic material. This paper describes eight siphonostomatoid copepod species discovered from those expeditions, all belonging to the family Dirivultidae.

Materials and Methods

The copepod material studied in this work was obtained from sediments and washings of invertebrates from hydrothermal vent fields on the Central Indian Ridge. Collections were performed using a video-guided hydraulic grab (Octopus, Germany) during the KIOST cruises at stations GTV1701 (19°33.398'S, 65°50.899'E, depth 2540 m)

and GTV1702 (19°33.387'S, 65°50.893'E, depth 2507 m) from the Solitaire vent field in July and August 2017, GTV1807 (19°33.395'S, 65°50.889'E, depth 2634 m) from the Solitaire vent field in June 2018, and GTV1809 (11°24.883'S, 65°25.425'E, depth 2022 m) from the Onnuri vent field (OVF) in June 2018. The collected specimens were initially preserved in 10% formalin for a couple of months, and then transferred to 80% ethanol. Prior to species description, selected copepod specimens were soaked in lactic acid and dissected using the reversed slide method by Humes and Gooding (1964). For the morphologic descriptions, the body length was measured from the anterior margin of the cephalothorax to the end of the caudal rami, excluding caudal setae. Type specimens have been deposited in the Marine Biodiversity Institute of Korea (MABIK), Seocheon, Korea.

Systematic accounts

Order Siphonostomatoida Thorell, 1859

Family Dirivultidae Humes and Dojiri, 1980

Genus *Aphotopontius* Humes, 1987

Aphotopontius kiost n. sp.

(Figs 1–3)

<http://zoobank.org/61F57C32-00BE-496D-9A72-C9D00C09A7AA>

Type material. Eleven females and three males from sediments at GTV1809 (11°24.883'S, 65°25.425'E, depth 2022 m), the Onnuri vent field (OVF) on the Central Indian Ridge in the Indian Ocean, 23 June 2018. Holotype (female, MABIK CR00244725) and paratypes (eight females and two males, MABIK CR00244726) have been deposited in the Marine Biodiversity Institute of Korea (MABIK), Seocheon. Dissected paratypes (two females and one male) are retained in the collection of the junior author.

Additional material examined. Forty-three females and nine males (one female and one male dissected) from washings of invertebrates (unidentified gastropods, bivalves and crustacean decapods) at GTV1702 (19°33.387'S, 65°50.893'E, depth 2507 m), the Solitaire vent area on the Central Indian Ridge, 01 August 2017; 20 females from washings of invertebrates at GTV1807 (19°33.395'S, 65°50.889'E, depth 2634 m), the Solitaire vent area on the Central Indian Ridge, 20 June 2018.

Female. Body (Fig. 1A) dorsoventrally flattened, 1.01 mm long in dissected paratype. Greatest width 515 µm across cephalothorax. Prosome 612 µm long, consisting of cephalothorax and three pedigerous somites. Posterolateral corners of cephalothorax pointed, those of three metasomal somites blunt or rounded. Ratio of length to width of prosome 1.19:1. Urosome (Fig. 1B) 5-segmented. Fifth pedigerous somite (first urosomal somite) 124 µm wide. Genital double-somite 128 × 146 µm, wider than long, with expanded proximal 1/3; genital aperture located dorsally at level of widest area at anterior third; lateral apex of this widest area blunt. Three free abdominal somites 46 × 93, 31 × 78, and 47 × 70 µm, respectively. Anal somite ornamented with two rows of spinules on ventral surface near posteroventral margin (Fig. 1C). Anal area located between anal somite and caudal rami. Caudal rami (Fig. 1C) close to each other, 83 × 29 µm, 2.86 times as long as wide, with six setae (setae II–VII) and triangular, serrate lamella on posteroventral margin; two mid-terminal setae pinnate, other four smaller setae naked.

Rostrum absent. Antennule (Fig. 1D) 288 µm long, 13-segmented; first segment being longest, fifth segment second longest; armature formula 15, 7, 1, 2, 4, 2, 2, 2, 2, 2 + aesthetasc, 2, 3, and 7 + aesthetasc; distal seta on fifth segment pinnate, other setae naked; aesthetasc on terminal segment small, indistinct. Antenna (Fig. 1E) with short, unarmed coxa; basis with row of several spinules near base of exopod. Exopod 22 × 7.8 µm, about 2.8 times as long as wide, with elongate distal and two shorter subdistal setae. Endopod 2-segmented; proximal segment unarmed, ornamented with row of spinules on outer margin; distal segment about half as long as proximal segment, armed with two spinulose spines (60 and 33 µm long, respectively), one distal, one lateral setae; distal half ornamented with spinules.

Oral cone short, stout. Mandible (Fig. 1F) represented by simple, flattened stylet bearing about ten teeth distally

and hyaline lamella along both margins. Maxillule (Fig. 1G) bilobed; outer lobe slightly shorter than inner lobe, with two distal and one subdistal setae; broader inner lobe with four setae distally and setules along inner margin. Maxilla (Fig. 1H) 2-segmented; proximal segment (syncoxa) unarmed but with basal pore; claw-like distal segment (basis) attenuated, with spinules (or setules) distally; large, spinulose seta present, arising between segments, with proximal articulation. Maxilliped (Fig. 1I) consisting of syncoxa, basis, and 2-segmented endopod; syncoxa subrectangular, with naked inner distal seta; basis with small inner seta and short setules on outer margin; proximal and distal endopodal segments armed with three and one setae, respectively; all setae naked; terminal claw weakly arched, 73 μm long, 2.2 times as long as distal endopodal segment, spinulose along inner margin.

Legs 1–3 (Fig. 2A–C) biramous, with 3-segmented rami. Leg 4 (Fig. 2D) with 3-segmented exopod and 2-segmented endopod. Inner coxal seta present in legs 1–3, but absent in leg 4. Inner spine on basis of leg 1 well-developed, spinulose, 43 μm long, extending to distal margin of first endopodal segment. Proximal and distal segments of leg 4 endopod 34×23 and 63×24 μm , respectively; distal segment with setules on outer and inner margins, its terminal spine setiform and 69 μm long. Armature formula for legs 1–4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1:	0-1	1-I	I-1; I-1; III, 2, 2	0-1; 0-2; 1, 2, 3
Leg 2:	0-1	1-0	I-1; I-1; III, I, 4	0-1; 0-2; 1, 2, 3
Leg 3:	0-1	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 1, I, 3
Leg 4:	0-0	1-0	I-1; I-1; III, I, 4	0-1; 0, I, 1

Leg 5 (Fig. 2E) unsegmented, but divisible by dorso-medial, non-sclerotized area into protopod and exopod; protopod about 37×18 μm , with elongate, naked dorsal seta; exopod 39×17 μm , about 2.3 times as long as wide, with three distal pinnate setae, longest one of latter three 100 μm long. Leg 6 (Fig. 2F) represented by short pinnate and minute setae in genital aperture.

Male. Body (Fig. 3A) narrower than that of female. Length of dissected paratype 644 μm . Prosoma 395 μm long, with greatest width 304 μm . Cephalothorax 259 μm long. Urosome 6-segmented. Genital somite 67×88 μm , distinctly wider than long, with rounded corners. Four abdominal somites 41×52 , 27×46 , 20×41 , and 27×40 μm , respectively. Anal somite with scattered spinules on posteroventral area. Caudal ramus (Fig. 3B) 41×17 μm , 2.41 times as long as wide, with serrate posteroventral margin.

Antennule (Fig. 3C) 11-segmented and curved medially; armature formula 1, 13, 7, 1 + spine, 2, 4, 2, 2, 2, aesthetasc, and 11. Fourth segment with strong outgrowth on anterior margin; spine on this segment with two longitudinal rows of spinules. Aesthetasc on penultimate segment relatively small, not extending beyond distal end of terminal segment.

Antenna, mandible, maxillule, maxilla, maxilliped, and legs 1–4 as in female.

Leg 5 (Fig. 3D) 2-segmented, but protopod (proximal segment) fused with somite, with elongate outer seta. Free exopod nearly quadrate, 20×17 μm , with three simple outer setae and two distal, knife-like setae; latter two setae 27 (ventral) and 26 μm (dorsal) long. Leg 6 (Fig. 5E) represented by two naked setae on spinulose genital operculum.

Etymology. The specific name *kiost* (noun) used in apposition is the abbreviation of the Korea Institute of Ocean Science and Technology (KIOST).

Remarks. In *Aphotopontius kiost* n. sp., the inner coxal setae are present in legs 1–3, but absent in leg 4. This feature is shared by other four congeners only: *A. acanthinus* Humes and Lutz, 1994, *A. atlanteus* Humes, 1996, *A. flexispinus* Humes, 1987, and *A. mammillatus* Humes, 1987. *Aphotopontius kiost* n. sp. is distinguishable from these four species by the different length/width ratio of the female caudal ramus; this ratio is 2.86 in *A. kiost* n. sp., whereas it is less than 2.0 in *A. acanthinus* and *A. atlanteus*, 4.2 in *A. flexispinus*, and 2.12 in *A. mammillatus* (see Humes and Lutz 1994; Humes 1987, 1996). As additional discrepant features, *A. atlanteus*, *A. flexispinus* and *A. mammillatus* have rounded lateral margins in the expanded anterior part of the genital double-somite, in contrast to *A. kiost* n. sp., in which the lateral margin bears an angular apex. Furthermore, *A. acanthinus* and *A. mammillatus* have a pointed inner distal extension on the basis of leg 1, in contrast to the absence of any pointed extension on the same region in *A. kiost* n. sp.

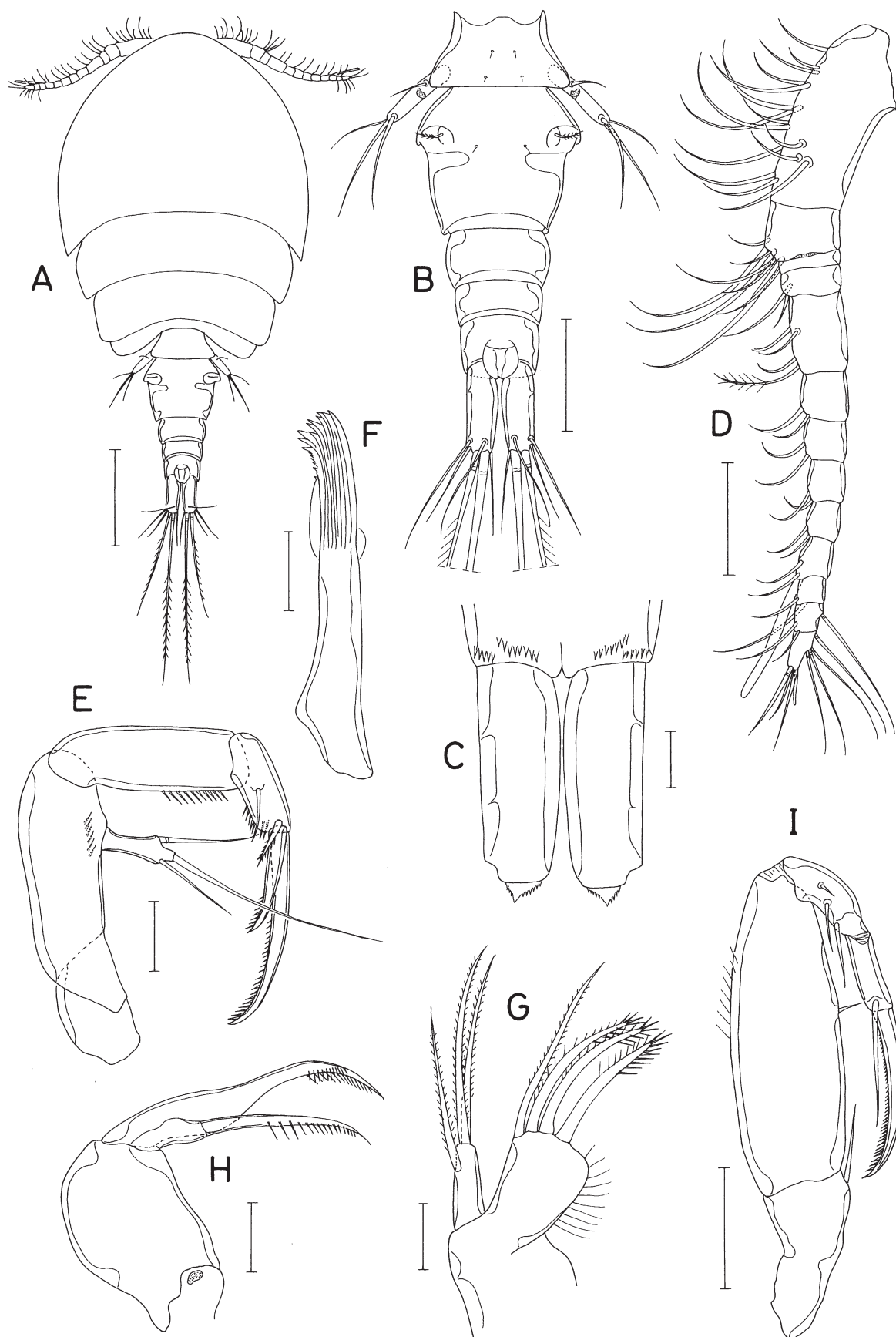


FIG. 1. *Aphotopontius kiost* n. sp., female. A, habitus, dorsal; B, urosome, dorsal; C, caudal rami, ventral; D, antennule; E, antenna; F, mandible; G, maxillule; H, maxilla; I, maxilliped. Scale bars: A = 0.2 mm; B = 0.1 mm; C, E–H = 0.02 mm; D, I = 0.05 mm.

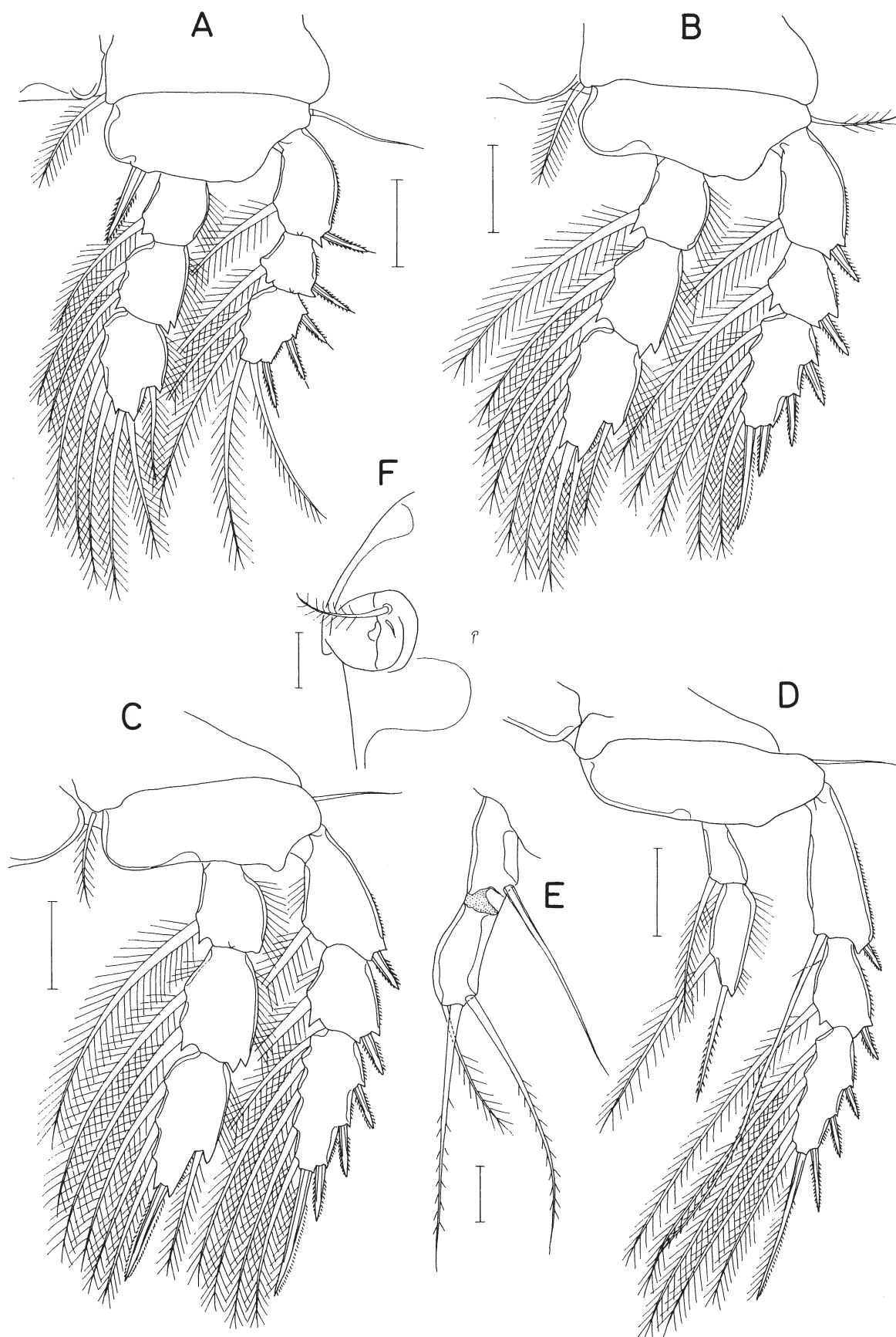


FIG. 2. *Aphotopontius kiost* n. sp., female. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5; F, genital aperture. Scale bars: A–D = 0.05 mm; E, F = 0.02 mm.

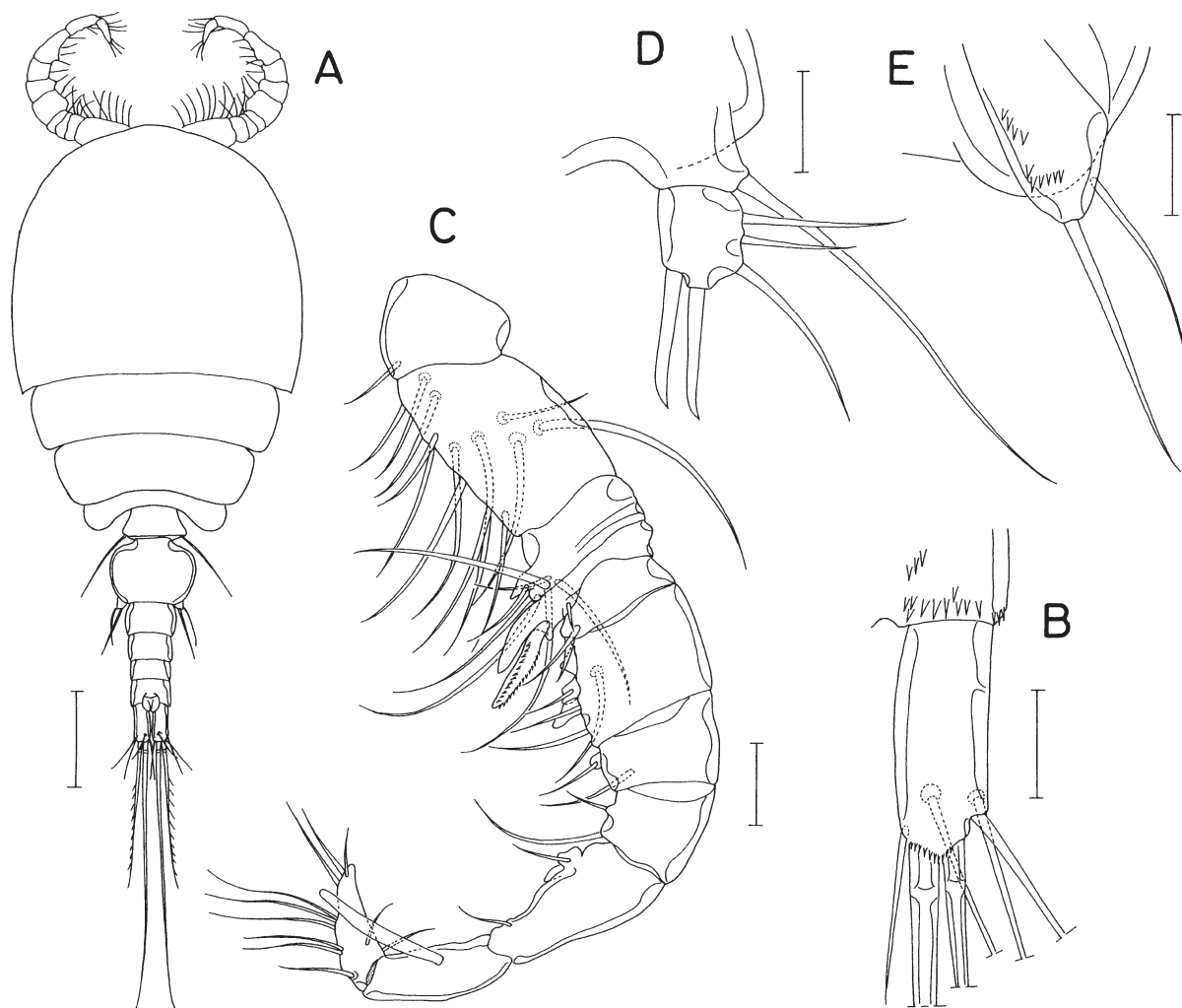


FIG. 3. *Aphotopontius kiost* n. sp., male. A, habitus, dorsal; B, left caudal ramus, ventral; C, antennule; D, left leg 5, ventral; E, left genital operculum. Scale bars: A = 0.1 mm; B–E = 0.02 mm.

***Aphotopontius muricatus* n. sp.**

(Figs 4, 5)

<http://zoobank.org/11F0AA95-F0EE-4D2B-9BF7-6E1B6355513A>

Material examined. One female (holotype, MABIK CR00244727, dissected and mounted on a slide) from washings of invertebrates, at GTV1807 (19°33.395'S, 65°50.889'E, depth 2634 m), the Solitaire hydrothermal vent area on the Central Indian Ridge in the Indian Ocean, 20 June 2018. Holotype was deposited in the Marine Biodiversity Institute of Korea (MABIK), Seocheon.

Female. Body (Fig. 4A) broad, flattened, 1.25 mm long. Greatest width 644 μ m across cephalothorax. Prosome 753 μ m long. Cephalothorax and three metasomal somites acutely pointed at posterolateral corners, 644, 531, 438, and 261 μ m wide, respectively. Ratio of length/ width of prosome 1.17:1. Urosome (Fig. 4B) 5-segmented. Fifth pedigerous somite (first urosomal somite) 84 \times 175 μ m, its posterolateral parts extended laterally, with angular distal corners. Genital double-somite 168 \times 139 μ m, 1.21 times longer than wide, constricted in middle of lateral margins, with dentiform process at posterolateral corners; genital aperture positioned dorsolaterally at 35% length of double-somite. Three abdominal somites 57 \times 82, 23 \times 71, and 57 \times 66 μ m, respectively; second abdominal somite less than half as long as first and anal somites. Anal somite (Fig. 4C) ornamented with scattered spinules on distal half of ventral surface. Caudal rami (Fig. 4C) elongate, close to each other, 6.61 times as long as wide (152 \times 23 μ m); armed with six setae, deduced from scars of setae, all of them positioned distally or subdistally.

Rostrum weak, easily destroyed, semicircular, with round posterior margin. Antennule (Fig. 4D) slender, longer than cephalothorax, 565 μm long, 12-segmented; articulation obscure between terminal and penultimate segments; first segment being longest and third segment shortest; armature formula 15, 10, 2, 4, 2, 2, 2, 2, 2 + aesthetasc, 1, 4, and 7; larger setae on first and second segments with multiple annulations; all setae naked. Antenna (Fig. 4E) slender, consisting of short, unarmed coxa, basis, 1-segmented exopod, and 2-segmented endopod; basis $128 \times 30 \mu\text{m}$, with longitudinal row of minute spinules along distal half. Exopod elongate, 8.4 times as long as wide ($76 \times 9 \mu\text{m}$), about 0.6 times as long as basis; with one terminal and two small subterminal setae. First endopodal segment $91 \times 23 \mu\text{m}$, unarmed, but ornamented with longitudinal row of minute spinules along inner side. Second endopodal segment $39 \times 17 \mu\text{m}$, less than half as long as first endopodal segment, armed with elongate, setiform terminal spine (235 μm long) and four setae, three of latter small, and ornamented with few setules.

Oral cone short, stout. Mandible (Fig. 4F) represented by simple, flattened stylet bearing irregular teeth distally and hyaline lamella at distal third. Maxillule (Fig. 4G) bilobed; outer lobe $34 \times 14 \mu\text{m}$, with two distal and one subdistal setae; inner lobe $58 \times 35 \mu\text{m}$, with protruded inner margin and distally armed with five setae, one of them minute. Maxilla (Fig. 4H) 2-segmented; proximal segment (syncoxa) proximally with short, wrinkled tube bearing pore at tip and distally one large setiform extension bearing several stiff setules subdistally; distal segment (basis) elongate, attenuated, with tuft of setules in middle, minute spinules along distal third of inner margin, setules along distal outer margin, and tipped with one large setule. Maxilliped (Fig. 5A) slender; syncoxa and basis fused, without articulation between them, bearing two setae on inner margin, about ten minute spinules near distal third of outer margin and few setules at proximal outer margin; endopod thin, 3-segmented, 38, 53, and 45 μm long, respectively, with three, one, and one setae, respectively; seta on second endopodal segment large, almost as long as combined endopodal segments; terminal claw elongate, 152 μm long, about 3.4 times as long as third endopodal segment.

Leg 1 (Fig. 5B) with 3-segmented rami. Inner distal spine on basis slender, 64 μm long. Outer spines on exopod slender. First and second exopodal segments setulose along outer margin. Endopod setulose along outer margin and flexed inwards between first and second segments; first segment about 1.6 times longer than wide; second and third segments broadened; outer distal corner of second segment bicuspid; outer one of two distal setae and third inner seta on third segment distinctly smaller than other setae on segment; inner one of two distal setae and first and second inner setae on third segment rather blunt at tip, with fine spinules along distal third of outer margin.

Leg 2 (Fig. 5C) with 3-segmented rami; exopod spinulose along outer margin. First exopodal segment with patch of spinules on anterior surface near base of inner seta. Endopod setulose along outer margin. Second endopodal segment with bicuspid outer distal corner.

Leg 3 (Fig. 5D) also with 3-segmented rami. Basis with prominent, digitiform process (indicated by arrowhead in Fig. 5D) on distal margin between bases of rami. Exopod as in leg 2. Endopod also as in leg 2, except armature of third endopodal segment bearing one distal spine and one outer and three inner setae.

Leg 4 (Fig. 5E) with 3-segmented exopod and 2-segmented endopod. Coxa lacking inner seta. Basis with small, attenuated process on distal margin between bases of rami. Both rami slender. Endopod as long as first exopodal segment; first and second endopodal segments 43 and 64 μm long, respectively; distal spine on second endopodal segment 133 μm long, longer than endopodal segments.

Armature formula for legs 1–4 as in *A. kiost* n. sp.

Leg 5 (Fig. 5F) distinctly 2-segmented. Protopod (first segment) 1.24 times as long as wide ($36 \times 29 \mu\text{m}$), with large outer distal seta (148 μm long). Exopod (second segment) 1.82 times as long as wide ($31 \times 17 \mu\text{m}$), gradually widened distally, armed with one outer subdistal seta (75 μm long) and two distal setae (86 and 40 μm long, respectively), shorter outer one of two latter naked, spiniform. Leg 6 (Fig. 5G) represented by one pinnate seta on genital operculum.

Male. Unknown.

Etymology. The specific name *muricatus* is derived from the Latin *muricat* (=pointed), referring to the pointed posterolateral corners of the cephalothorax and metasomal somites.

Remarks. *Aphotopontius muricatus* n. sp. is similar to *A. mammillatus* Humes, 1987, which was redescribed by Ivanenko and Heptner (1998), in having a female genital double-somite that is distinctly longer than wide, with a constriction in the middle and a dentiform process at each posterolateral corner. Otherwise, the new species is readily separable from *A. mammillatus* and other congeners due to three striking morphological features: (1) the antenna bears an elongate exopod that is longer than half the length of the basis, (2) the syncoxa and the basis of the maxilliped are fused to each other, and (3) the endopod of leg 1 is flexed inwards.

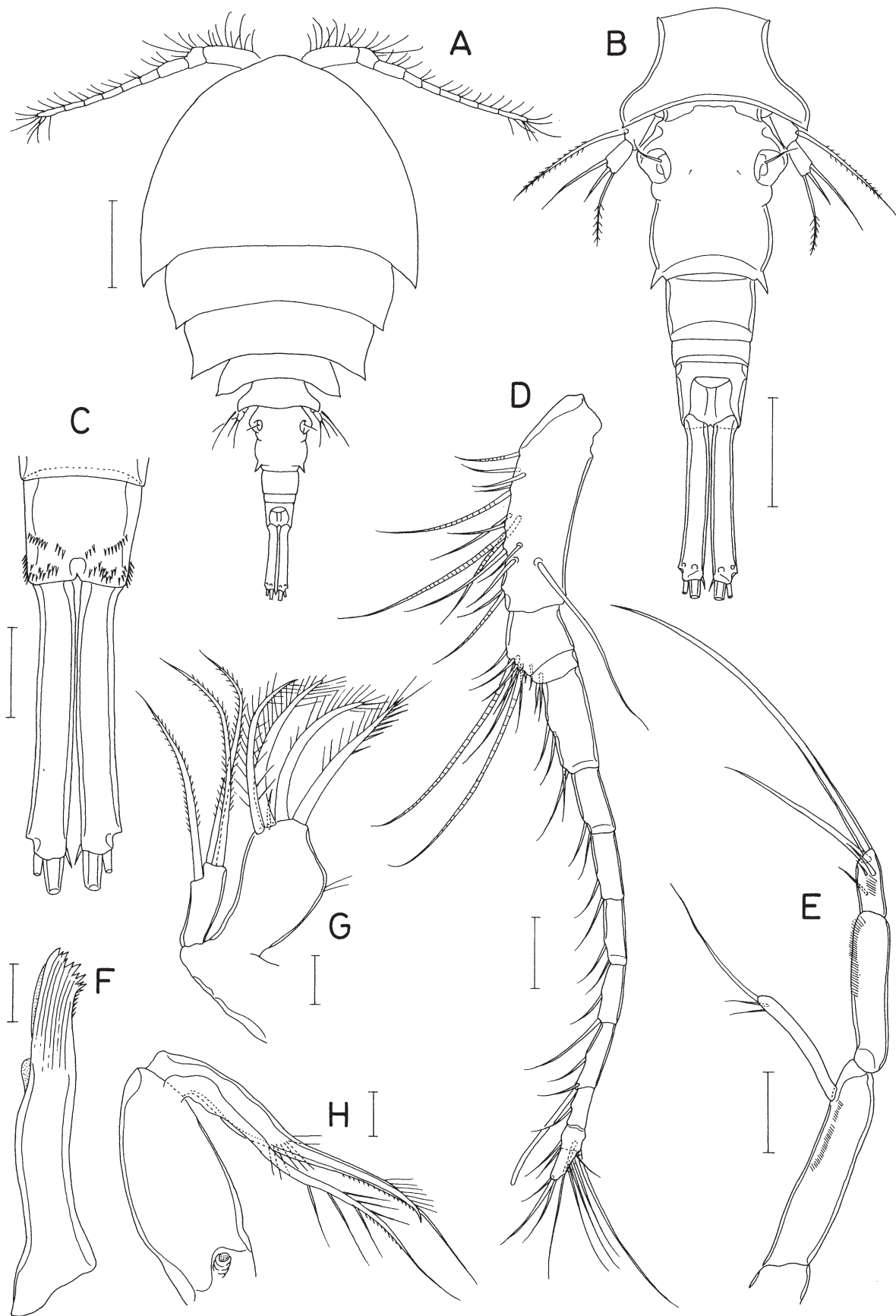


FIG. 4. *Aphotopontius muricatus* n. sp., female. A, habitus, dorsal; B, urosome, dorsal; C, anal somite and caudal rami, ventral; D, antennule; E, antenna; F, mandible; G, maxillule; H, maxilla. Scale bars: A = 0.2 mm; B = 0.1 mm; C–E = 0.05 mm; F–H = 0.02 mm.

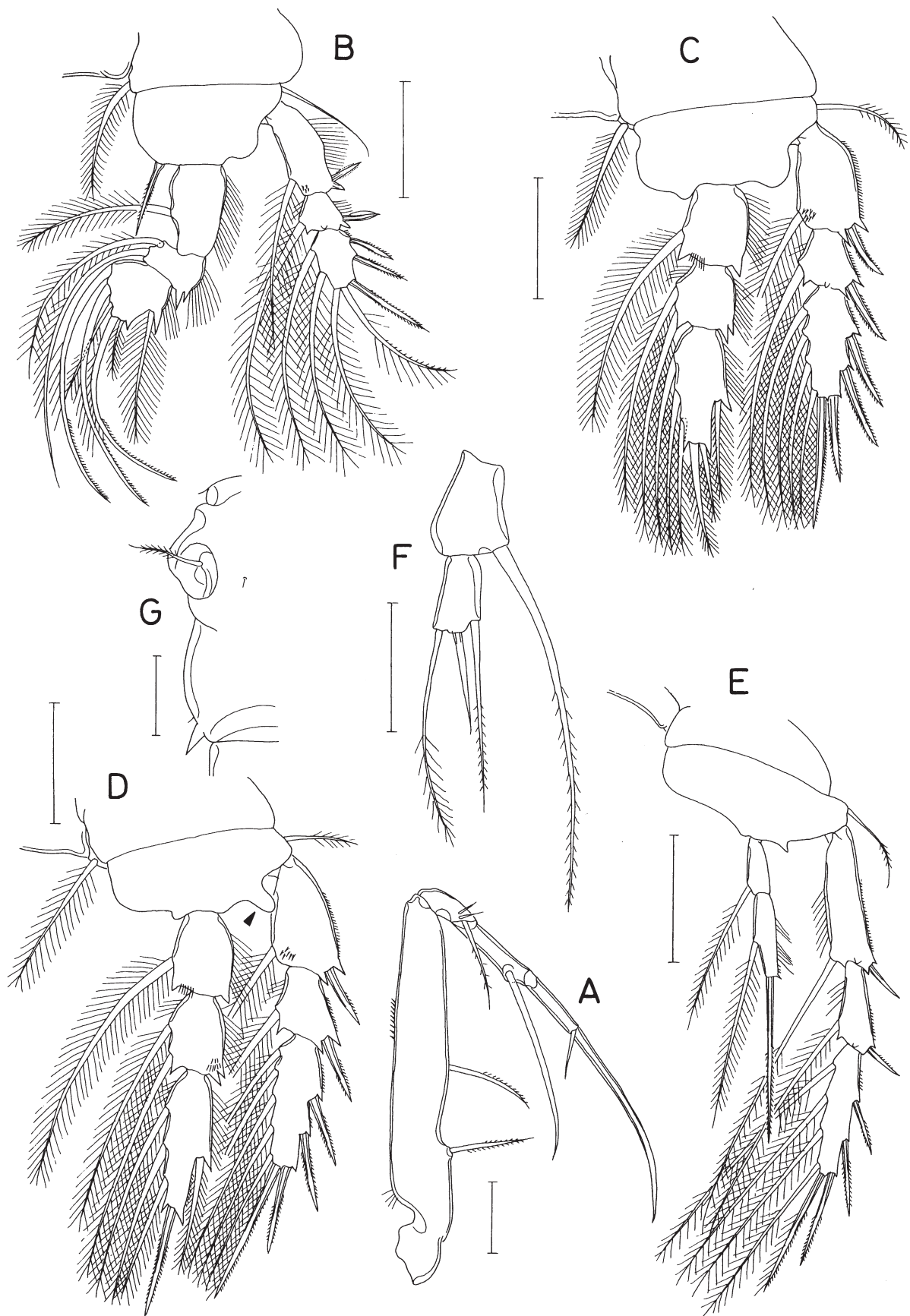


FIG. 5. *Aphotopontius muricatus* n. sp., female. A, maxilliped; B, leg 1; C, leg 2; D, leg 3; E, leg 4; F, leg 5; G, left side of genital double-somite, dorsal. Scale bars: A, F, G = 0.05 mm; B–E = 0.1 mm.

Aphotopontius limatulus Humes, 1987

(Figs 6–8)

Material examined. One female and one male from washings of invertebrates at GTV1702 (19°33.387'S, 65°50.893'E, depth 2507 m), the Solitaire vent field in the Indian Ocean, 01 August 2017; two females from sediments at GTV1701 (19°33.398'S, 65°50.899'E, depth 2540 m), the Solitaire vent field, 31 July 2017; seven females from washing of invertebrates, at GTV1807 (19°33.395'S, 65°50.889'E, depth 2634 m), the Solitaire vent field, 20 June 2018; one female from sediments at GTV 1809 (11°24.883'S, 65°25.425'E, depth 2022 m) from the Onnuri vent field, 23 June 2018.

Female. Body (Fig. 6A) rather narrow, 1.17 mm long. Prosome oval, 740 µm long, with greatest width 555 µm. Cephalothorax 416 µm long, wider than long, with pointed posterolateral corners. Second pedigerous somite also with pointed posterolateral corners. Urosome (Fig. 6B) slender. Fifth pedigerous somite tapering posterolaterally, 157 µm wide, wider than genital double-somite, with angular lateral apices. Genital double-somite 109 × 144 µm, much wider than long; anterior two-thirds broader than posterior third; genital aperture located dorsolaterally, slightly posterior to midlength. Three free abdominal somites 39 × 87, 22 × 78, and 43 × 70 µm, respectively. Anal somite narrowing distally, with patch of spinules on posteroventral surfaces near bases of caudal rami. Caudal ramus (Fig. 6C) elongate, 177 × 20 µm, 8.85 times as long as wide, with three patches of spinules on ventral surface (two patches near middle and one on distal regions), and armed with six setae distally; two mid-terminal setae weakly pinnate, other four setae naked; inner distal seta very small, spinule-like.

Rostrum (Fig. 6D) distinct, tapering, with rounded posterior apex. Antennule (Fig. 6E) slender, elongate, 617 µm long, and 11-segmented; first segment longest; armature formula 15, 10, 2, 4, 2, 2, 2, 2, 2 + aesthetasc, 6, and 7; setae small and naked. Antenna (Fig. 6F) slender. Short syncoxa unarmed. Basis with setules on inner margin and row of fine spinules on outer margin near base of exopod. Exopod small, 12 × 5 µm, with two unequal setae distally. Endopod 2-segmented; first segment 51 × 19 µm, with setules along inner and outer margins; second segment 21 × 16 µm, with four setiform elements, inner subterminal one rudimentary.

Oral cone stout. Mandible (Fig. 6G) with about ten teeth distally and small hyaline lamella at distal third. Maxillule (Fig. 6H) with three setae on outer lobe and four setae + one small setule on inner lobe. Maxilla (Fig. 6I) with a pore at base of syncoxa; endopod attenuated, with setules at distal region, distal one of these setules longer than others; setae between syncoxa and basis large, longer than basis and ornamented with long setules. Maxilliped (Fig. 6J) 4-segmented; inner seta of syncoxa large, 90 µm long, finely spinulose along its proximal margin. Inner seta on basis naked, 70 µm long, and directed proximally; first endopodal segment with two setae and one thin setule; second endopodal segment 30 µm long, with one seta distally; terminal claw slender, 105 µm long, and finely spinulose along inner margin.

Legs 1–3 (Fig. 7A–C) with three segmented rami. Leg 4 (Fig. 7D) with 3-segmented exopod and 2-segmented endopod. Inner coxal seta present in legs 2 and 3, but lacking in legs 1 and 4. Inner spine on basis of leg 1 moderately slender and 47 µm long. Two distal setae on third endopodal segment of leg 2 spiniform. Leg 4 with slender rami; inner seta on first exopodal segment with fine spinules along its distal half; first endopodal segment 54 × 35 µm, its inner seta shorter than second endopodal segment; second endopodal segment 133 × 28 µm, setulose along proximal half of both margins and finely spinulose along distal half of outer margin; distal spine 98 µm long, with fine spinules on both margins. Armature formula of legs 1–4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1:	0-0	1-I	I-1; I-1; III, 2, 2	0-1; 0-2; 1, 2, 3
Leg 2:	0-1	1-0	I-1; I-1; III, I, 4	0-1; 0-2; 1, 2, 3
Leg 3:	0-1	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 1, I, 3
Leg 4:	0-0	1-0	I-1; I-1; III, I, 4	0-1; 0, I, 1

Leg 5 (Fig. 7E) clearly 2-segmented; protopod 43 × 28 µm, with naked outer seta; exopod 30 × 20 µm, with three naked setae. Leg 6 represented by one small seta in genital aperture (Fig. 6B).

Male. Body (Fig. 8A) more slender than that of female. Length 1.01 mm. Prosome 602 µm long and greatest width 442 µm. First three prosomal somites with acutely pointed posterolateral corners. Urosome 6-segmented.

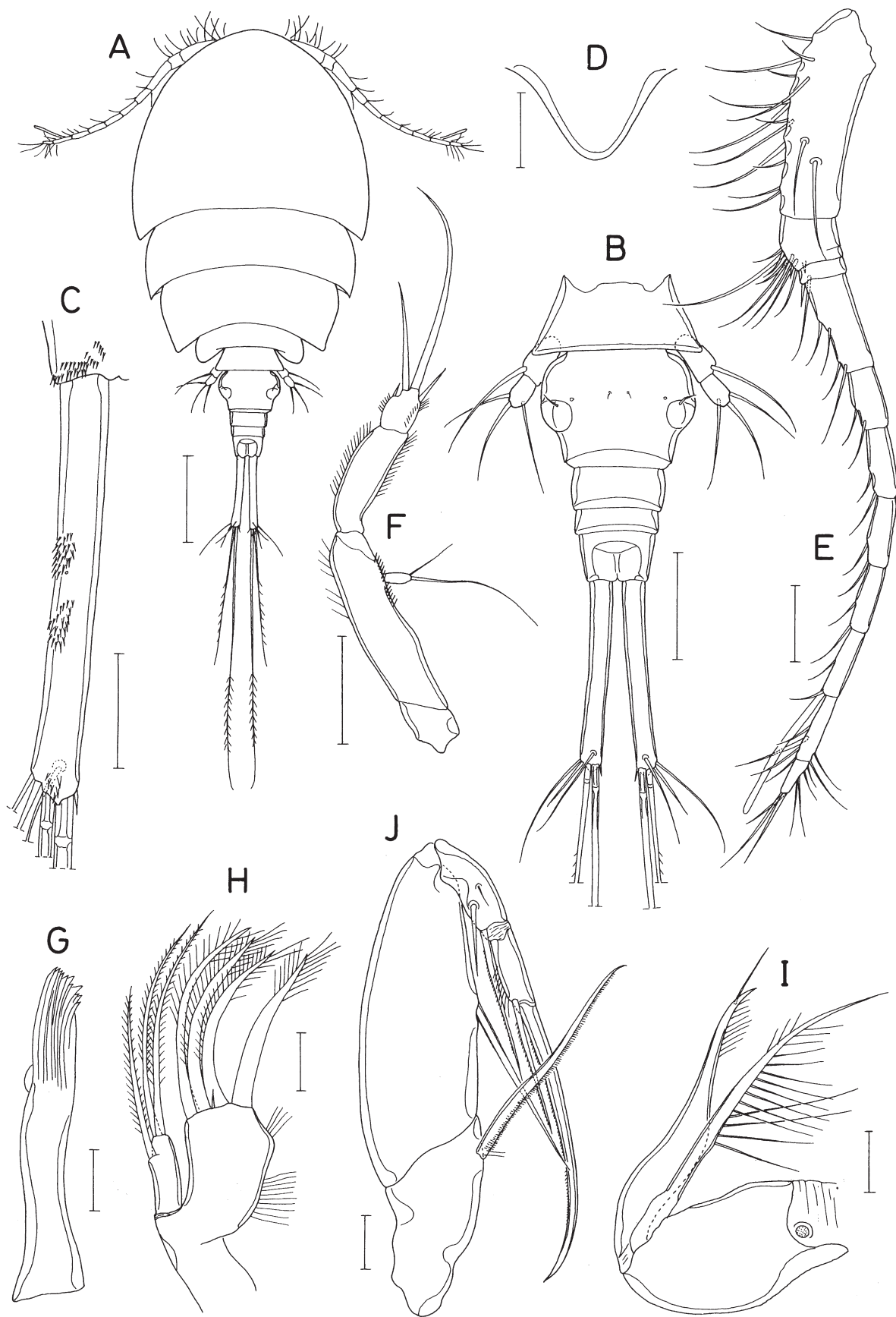


FIG. 6. *Aphotopontius limatulus* Humes, female. A, habitus, dorsal; B, urosome, dorsal; C, right caudal ramus, ventral; D, rostrum; E, antennule; F, antenna; G, mandible; H, maxillule; I, maxilla; J, maxilliped. Scale bars: A = 0.2 mm; B = 0.1 mm; C–F = 0.05 mm; G–J = 0.02 mm.

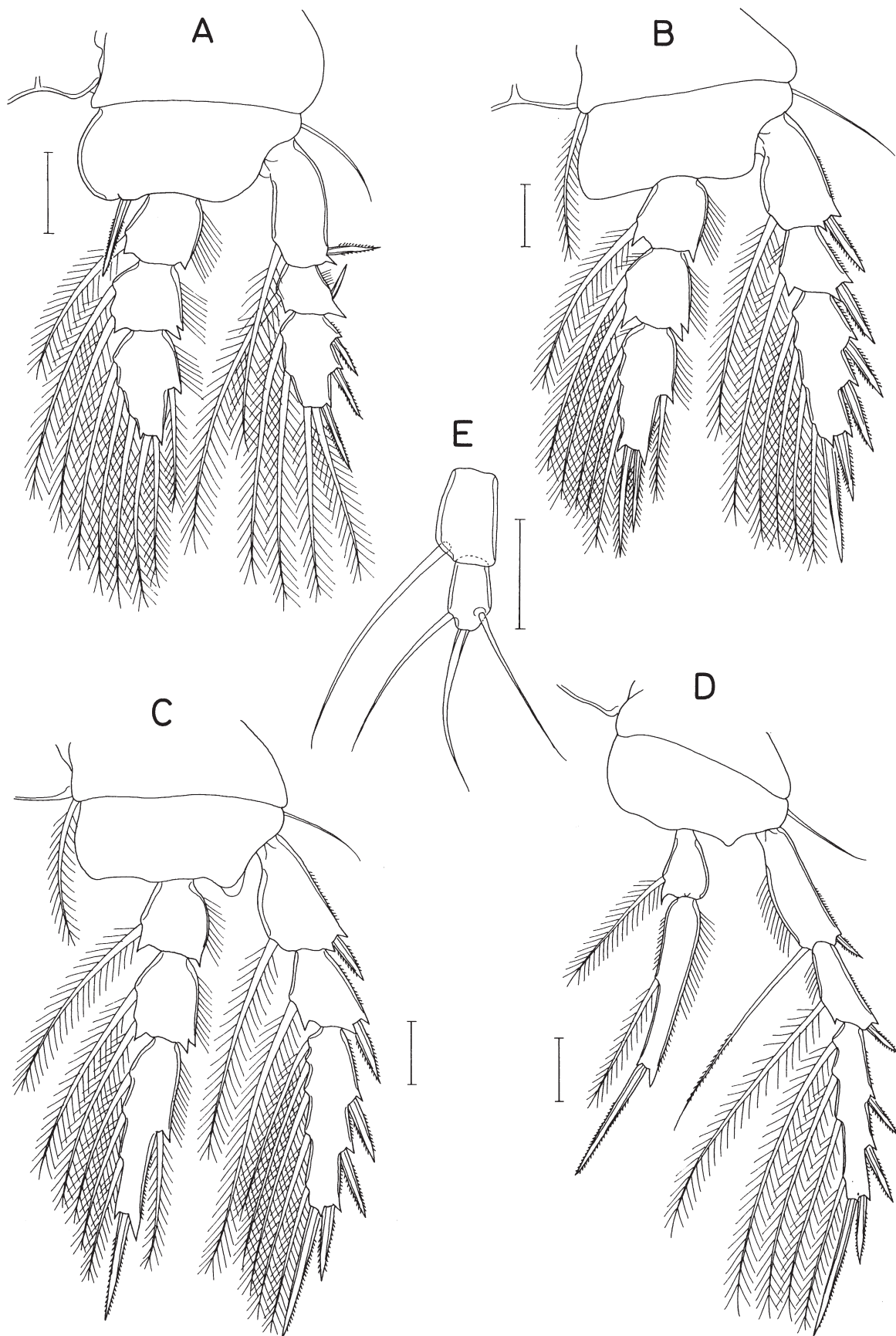


FIG. 7. *Aphotopontius limatulus* Humes, female. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5. Scale bars: 0.05 mm.

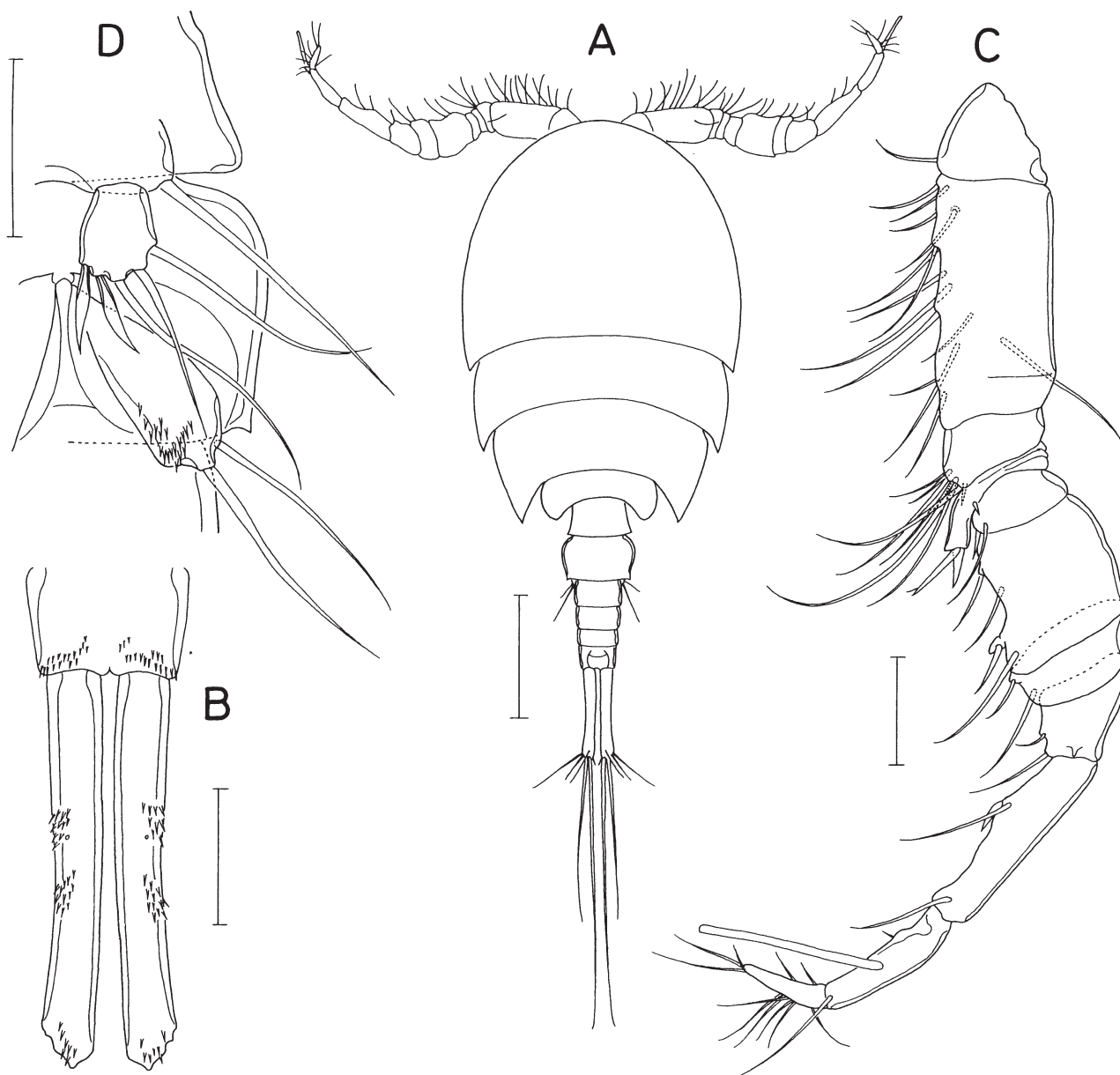


FIG. 8. *Aphotopontius limatulus* Humes, male. A, habitus, dorsal; B, anal somite and caudal rami, ventral; C, antennule; D, left legs 5 and 6, ventral. Scale bars: A = 0.2 mm; B–D = 0.05 mm.

Fifth pedigerous somite 102 μm wide. Genital somite 76 \times 113 μm , much wider than long, with spinules on ventral surface of genital operculum (Fig. 8D). Four abdominal somites 46 \times 73, 34 \times 68, 24 \times 64, and 40 \times 60 μm , respectively. Caudal ramus (Fig. 8B) 146 \times 20 μm , 7.30 times as long as wide. Anal somite and caudal rami with spinules on ventral surface, as in female.

Rostrum as in female. Antennule (Fig. 8C) 11-segmented; armature formula 1, 14, 8, 3, 2, 4, 2, 2, 2, 2 + aesthetasc, and 11; fourth segment with outgrowth tipped by two spiniform elements and with one minute seta; proximal seta on penultimate segment minute, obscure; antepenultimate segment with additional spiniform process. Antenna as in female.

Mandible, maxillule, maxilla, maxilliped, and legs 1–4 as in female.

Leg 5 (Fig. 8D) 2-segmented; protopod short unarticulated from somite, with one large outer seta; exopod 27 \times 21 μm , with three long outer setae and two inner knife-like setae. Leg 6 (Fig. 8D) represented by two long setae on genital operculum.

Remarks. *Aphotopontius limatulus* Humes, 1987 has previously been reported from the East Pacific Rise and Galapagos Rift in the Pacific Ocean (Humes 1998). Our material from the Central Indian Ridge does not differ

significantly from the type specimens. The only notable differences were in the caudal ramus and antennule. The length-to-width ratio of the caudal ramus of the type specimens was described 9.94 in the female and 8.6 in the male, while it is 8.85 and 7.30 in our female and male specimens, respectively. The two ventral patches of spinules on the mid-region of the caudal ramus are not mentioned in the original description. The antennule of the type specimens is described as 10-segmented in the female and 12-segmented in the male, whereas it is 11-segmented in both sexes of our specimens. We consider these differences to be within species variation or artificial and insufficient to separate them as different species.

Four species in the Dirivultidae have been recorded as transoceanic, from both the Atlantic and Pacific oceans: *Aphotopontius forcipatus* Humes, 1987, *Stygiopontius mirus* Humes, 1996, *S. pectinatus* Humes, 1987, and *S. rimi-vagus* Humes, 1997 (Humes 1990, 1996, 1998; Gollner *et al.* 2010). Here, *A. limatulus* is reported as an additional transoceanic species from the Pacific and Indian Oceans.

Genus *Benthoxynus* Humes, 1984

Benthoxynus constrictus n. sp.

(Figs 9, 10)

<http://zoobank.org/13B0DBCD-6362-49E6-BE95-0509CBCB4863>

Material examined. Two females from washings of invertebrates at GTV1702 (19°33.387'S, 65°50.893'E, depth 2507 m), the Solitaire vent field on the Central Indian Ridge, 01 August 2017. Holotype (female, MABIK CR00244728) has been deposited in the Marine Biodiversity Institute of Korea (MABIK), Seocheon. Dissected paratype is retained in the collection of the junior author.

Female. Body (Fig. 9A) narrow, 1.78 mm long. Prosoma oviform, 930 × 750 µm. Cephalothorax 632 µm long, with tapering posterolateral corners. Second to fourth pedigerous somites with rounded posterolateral corners. Urosome (Fig. 9B) slender. Fifth pedigerous somite laterally constricted in middle, with dorsal posterolateral extensions. Genital double-somite rhomboidal, 222 × 236 µm, widest at proximal third; genital aperture located dorsolaterally slightly posterior to widest region. Three free abdominal somites 139 × 113, 90 × 100, and 90 × 102 µm, respectively. Abdominal somite and caudal rami smooth, without setules or spinules on all surfaces. Caudal rami (Fig. 9C) slightly divergent; each ramus 209 × 43 µm, 4.86 times as long as wide, armed with six setae (setae II–VII); dorsal seta located subdistally and other five setae on distal margin; two larger mid-terminal setae weakly pinnate along distal half; inner distal seta characteristically small, obscure.

Rostrum absent. Antennule (Fig. 9D) 710 µm long and 12-segmented; third segment longest, with five transverse sclerotization bands on one surface (not shown in Fig. 9D); armature formula 1, 2, 12, 10, 2, 4, 2, 2, 2, 2, 2 + aesthetasc, and 13; aesthetasc on penultimate segment slender, slightly longer than terminal segment. Antenna (Fig. 9E) with short, unarmed syncoxa. Basis smooth. Exopod small, 19 × 9 µm, with three setae distally. Endopod 2-segmented; proximal segment 98 × 43 µm, unarmed; distal segment 72 × 35 µm, with four setae (one small inner, two subdistal, and one large distal) and several setules near base of outer subdistal seta.

Oral cone stout as usual in the family. Mandible (Fig. 9F) as flattened stylet, with more than ten teeth distally and hyaline lamella along distal fourth of inner margin. Maxillule (Fig. 9G) bilobed; outer lobe with four setae (three distal and one subdistal); inner lobe with strongly protruded inner margin and four distal setae; both outer and inner lobes smooth without setules or spinules. Maxilla (Fig. 9H) 2-segmented; syncoxa unarmed, with pore at basal region; basis elongate, with fine spinules and setules at distal region, one of setules large; one large seta present, arising between syncoxa and basis. Maxilliped (Fig. 9I) 5-segmented; syncoxa with one inner distal seta of 42 µm long; basis with inner seta of 71 µm long; endopod 3-segmented, with two, one, and one setae, respectively; two setae on first endopodal segment minute, obscure; third endopodal segment 52 µm; terminal claw 174 µm long, weakly arched, with spinules along distal half of inner margin.

Legs 1–4 (Figs. 10A–D) lacking inner coxal seta; outer seta on basis thin and naked; setae of these legs, especially those of endopod, swollen in proximal third and weakly pinnate in distal half. Second exopodal segment of leg 1 small, with outer spine and inner seta; all of other elements on leg 1 setiform. Inner distal seta on basis of leg 1 minute, needle-like. First endopodal segment of leg 3 unarmed, lacking inner seta. First and second endopodal

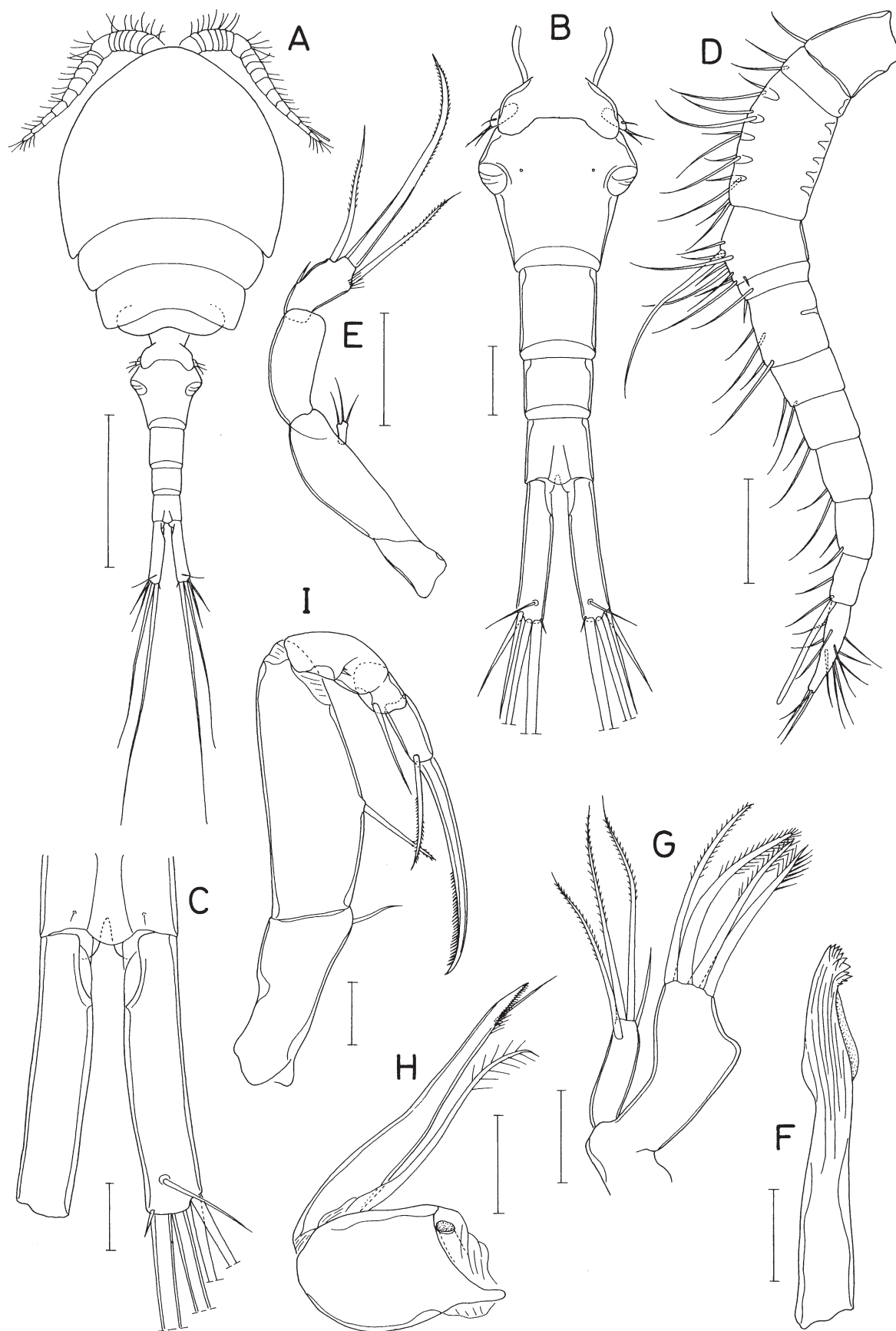


FIG. 9. *Benthoxynus constrictus* n. sp., female. A, habitus, dorsal; B, urosome, dorsal; C, caudal rami, dorsal; D, antennule; E, antenna; F, mandible; G, maxillule; H, maxilla; I, maxilliped. Scale bars: A = 0.5 mm; B, D, E = 0.1 mm; C, F–I = 0.05 mm.

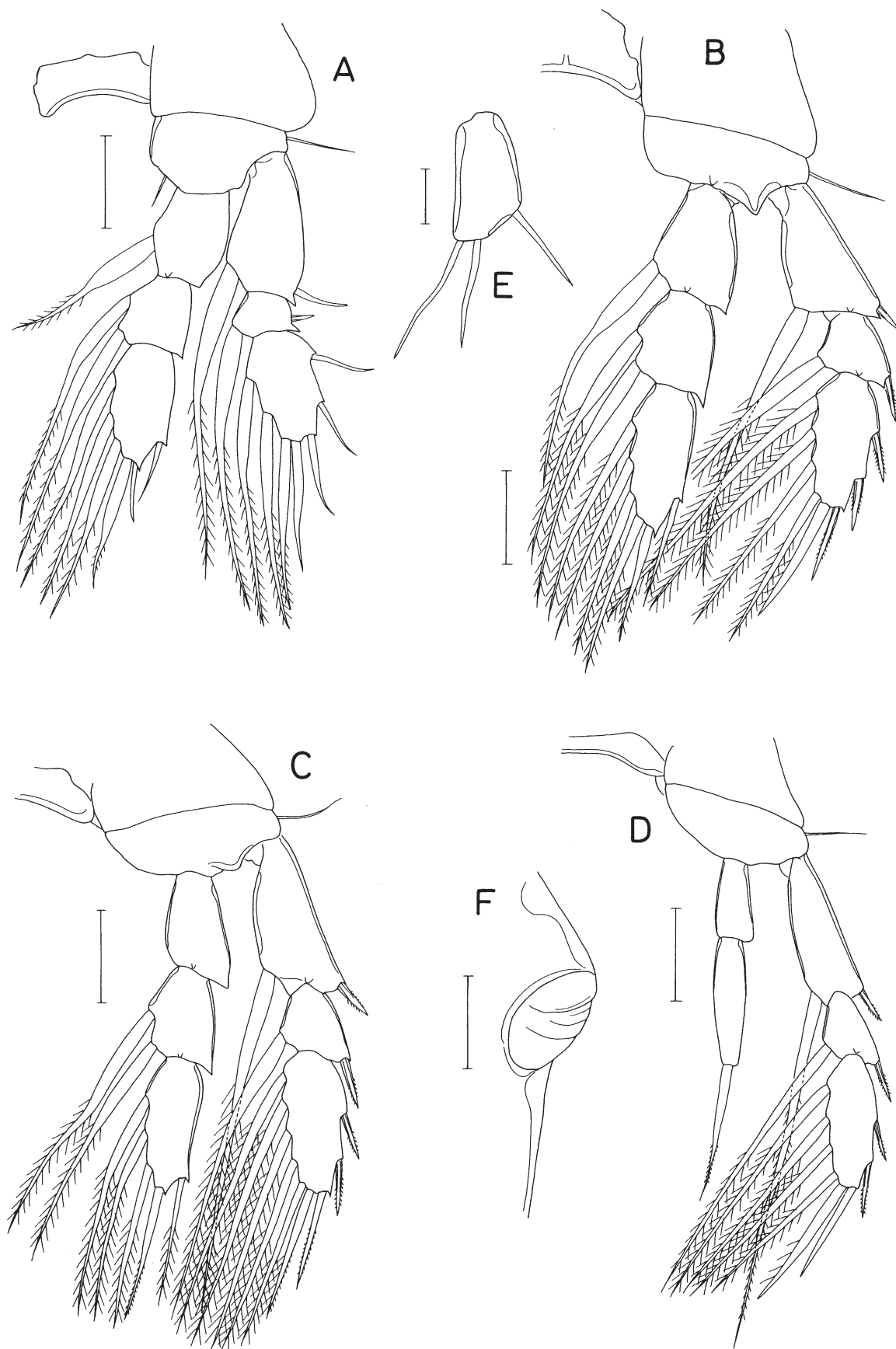


FIG. 10. *Benthoxynus constrictus* n. sp., female. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5; F, right genital aperture. Scale bars: A–D = 0.1 mm; E = 0.02 mm; F = 0.05 mm.

segments of leg 4 smooth, 86×41 and 133×35 μm , respectively; terminal seta 145 μm long. Armature formula of legs 1–4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1:	0-0	1-1	1-1; 1-1; 3, 1, 3	0-1; 0-2; 1, 2, 3
Leg 2:	0-0	1-0	I-1; I-1; III, I, 4	0-1; 0-2; 1, 2, 3
Leg 3:	0-0	1-0	I-1; I-1; III, I, 5	0-0; 0-2; 1, I, 3
Leg 4:	0-0	1-0	I-1; I-1; III, I, 4	0-0; 0, I, 0

Leg 5 (Fig. 10E) 1-segmented, clearly articulated from somite, 45×23 μm , about twice as long as wide, with three naked setae (one dorsal and two distal). Leg 6 absent (Fig. 10F).

Male. Unknown.

Etymology. The specific name *constrictus* refers to the lateral constriction of the fifth pedigerous somite.

Remarks. *Benthoxynus spiculifer* Humes, 1984 and *B. tumidiseta* Humes, 1989, the two known members of the genus, were recorded from hydrothermal vent fields in the East Pacific. These two congeners of *B. constrictus* n. sp. have the following features which are useful for differentiating them from the new species:

(1) Leg 5 is lobate, unarticulated from the fifth pedigerous somite (vs. free in *B. constrictus* n. sp.).

(2) The antennule is 18-segmented in *B. spiculifer* and 11-segmented in *B. tumidiseta* (vs. 12-segmented in *B. constrictus* n. sp.).

(3) The caudal ramus is longer than that of n. sp., 240 μm in *B. spiculifer* and 313 μm in *B. tumidiseta* (Humes, 1984, 1989) (vs. 209 μm in *B. constrictus* n. sp.), although their bodies are smaller than that of *B. constrictus* n. sp. (recorded as 1.68 and 1.67 mm long, respectively, in their original descriptions).

(4) The fifth pedigerous somite is not constricted laterally (vs. strongly constricted in *B. constrictus* n. sp.).

Genus *Stygiopontius* Humes, 1987

Stygiopontius spinifer n. sp.

(Figs 11, 12)

<http://zoobank.org/BBD02F2A-B2ED-4EEF-A084-EACA8134C4BE>

Material examined. Fifty-five females from sediments at GTV1809 ($11^{\circ}24.883'S$, $65^{\circ}25.425'E$, depth 2022 m), the Onnuri vent field on the Central Indian Ridge, 23 June 2018. Holotype (female, MABIK CR00244729) and paratypes (30 females, MABIK CR00244730) have been deposited in the Marine Biodiversity Institute of Korea (MABIK), Seochon. Other specimens are retained in the collection of the junior author.

Additional material examined. Ten females (one female dissected) from washings of invertebrates at GTV1702 ($19^{\circ}33.387'S$, $65^{\circ}50.893'E$, depth 2507 m), the Solitaire vent field on the Central Indian Ridge, 01 August 2017; four females from washings of invertebrates at GTV1807 ($19^{\circ}33.395'S$, $65^{\circ}50.889'E$, depth 2634 m), the Solitaire vent field on the Central Indian Ridge, 20 June 2018.

Female. Body (Fig. 11A) dorsoventrally flattened, 1.51 mm long. Prosoma 865×742 μm , oviform in dorsal view; posterolateral corners pointed in cephalothorax and second pedigerous somite, but rounded in third and fourth pedigerous somites. Cephalothorax 523 μm long. Urosome (Fig. 11B) 5-segmented. Fifth pedigerous somite trap-ezoidal, 199 μm wide, with blunt lateral apices. Genital double-somite 184×180 μm ; anterior third broader than posterior two thirds, with claw-like, posteriorly directed lateral process on both sides near genital aperture; narrower posterior part gradually narrowing posteriorly. Three free abdominal somites 85×119 , 61×109 , and 61×107 μm , respectively. Anal somite with five or six spinules along both sides of posteroventral border (Fig. 11C). Caudal rami (Fig. 11C) parallel; each ramus 97×45 μm measured in ventral view, 2.16 times as long as wide, with six setae (setae II–VII); two larger mid-terminal setae pinnate along distal two thirds; inner terminal seta unilaterally pinnate along inner margin; other three setae naked.

Rostrum absent. Antennule (Fig. 11D) 430 μm long and 12-segmented; third segment longest; armature formula

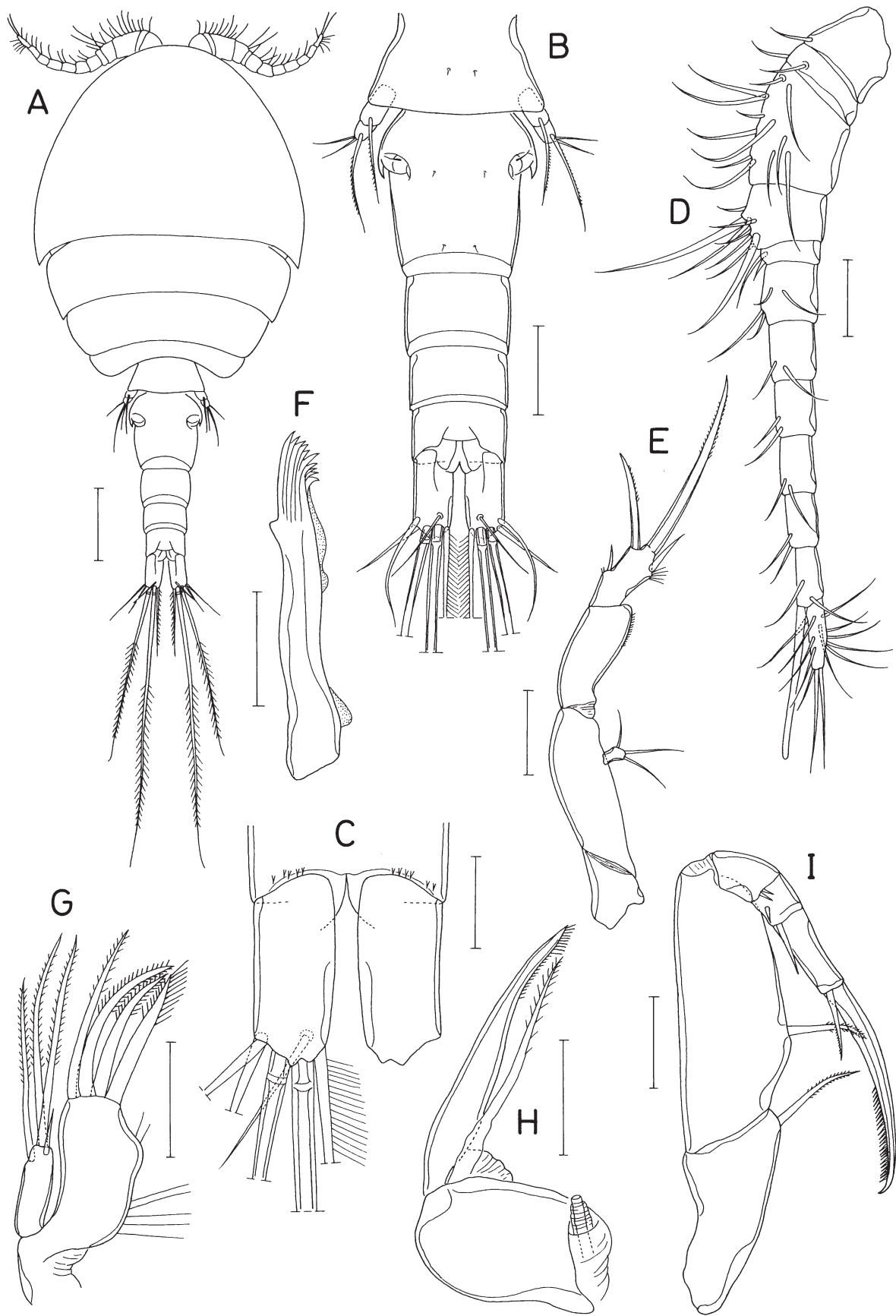


FIG. 11. *Stygiopontius spinifer* n. sp., female. A, habitus, dorsal; B, urosome, dorsal, C, caudal rami, ventral; D, antennule; E, antenna; F, mandible; G, maxillule; H, maxilla; I, maxilliped. Scale bars: A = 0.2 mm; B = 0.1 mm; C–I = 0.05 mm.

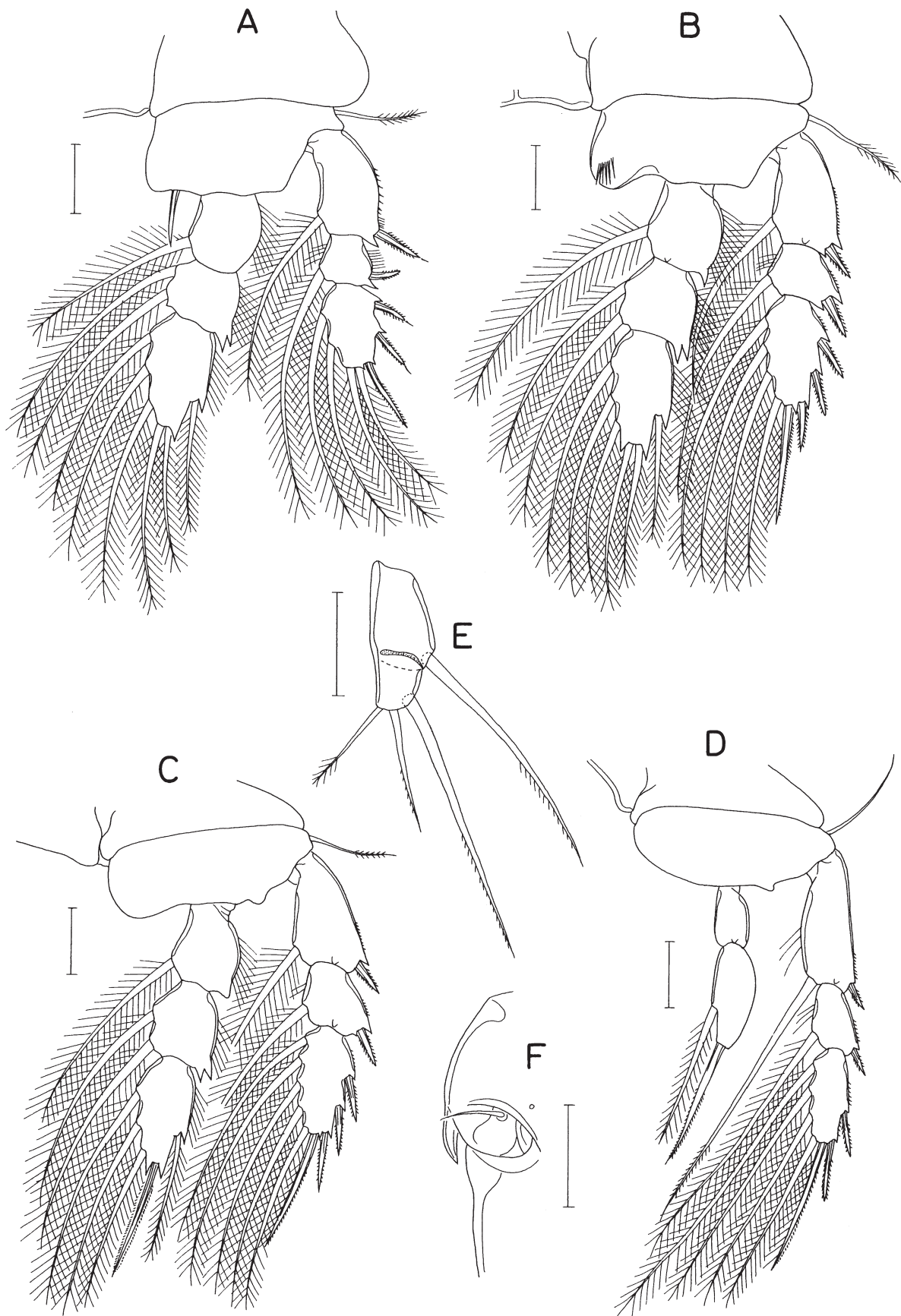


FIG. 12. *Stygiopontius spinifer* n. sp., female. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5; F, left genital aperture. Scale bars: 0.05 mm.

1, 2, 12, 8, 2, 4, 2, 2, 2, 2, 2 + aesthetasc, and 13; aesthetasc on penultimate segment more than twice as long as terminal segment; setae generally short, all of them naked. Antenna (Fig. 11E) with short, unarmed syncoxa. Basis smooth. Exopod small, $13 \times 9 \mu\text{m}$, with three setae. Endopod 2-segmented; proximal segment $62 \times 29 \mu\text{m}$, with fine spinules along distal half of outer margin; distal segment $43 \times 21 \mu\text{m}$, with two spines, two setae, and few setules.

Oral cone stout. Mandible (Fig. 11F) with about ten teeth distally, one blunt process near distal fourth of outer margin, and two hyaline lamellae (proximal and distal) on inner margin. Maxillule (Fig. 11G) bilobed; outer lobe with four setae, including three large, weakly pinnate and one small, naked ones; inner lobe with four setae distally and several setules on inner margin. Maxilla (Fig. 11H) as usual in the genus; seta between segments not extending over basis. Maxilliped (Fig. 11I) 5-segmented; syncoxa and basis each with one inner seta, 54 and 45 μm long, respectively, both spinulose in distal half; endopod with two, two, and one setae, respectively, on first to third segments; third segment 45 μm long; terminal claw 117 μm long, weakly arched, with spinules along distal half of inner margin.

Legs 1–4 (Fig. 12A–D) without inner seta on coxa. Second endopodal segment of legs 1–3 with bicuspid outer distal corner. Inner distal spine on basis of first leg 40 μm long and slender. Basis of leg 2 with five spinules on inner side. Leg 4 (Fig. 12D) with three spines and four setae on third exopodal segment; first endopodal segment $45 \times 26 \mu\text{m}$; second endopodal segment $76 \times 32 \mu\text{m}$, its distal spine 100 μm long. Armature formula of legs 1–4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1:	0-0	1-I	I-1; I-1; III, 2, 2	0-1; 0-2; 1, 2, 3
Leg 2:	0-0	1-0	I-1; I-1; III, I, 4	0-1; 0-2; 1, 2, 3
Leg 3:	0-0	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 1, I, 3
Leg 4:	0-0	1-0	I-1; I-1; II, I, 4	0-0; 0, I, 1

Leg 5 (Fig. 12E) unsegmented but divided into proximal and distal parts by unsclerotized band on both surfaces; proximal part $46 \times 32 \mu\text{m}$, with large, feebly pinnate seta; distal part $23 \times 23 \mu\text{m}$, with three setae, larger outer seta twice as long as two smaller inner setae. Leg 6 (Fig. 12F) represented by one naked seta in genital aperture.

Male. Unknown.

Etymology. The specific name *spinifer*, Latin *spin* (=a spine) and *fero* (=to carry), alludes to the spiniform process on the lateral margins of the genital double-somite, as in several congeners.

Remarks. The genus *Stygiopontius* is characterized by the combination of the features, as follows: (1) the endopod of leg 1 is three-segmented in both sexes; (2) the first endopodal segment of leg 3 is armed with an inner seta; (3) the first endopodal segment of leg 4 lacks an inner seta; and (4) the second endopodal segment of leg 4 is armed with one distal spine and one inner seta. In the genus *Stygiopontius*, seven species are known to have, like *S. spinifer* n. sp., two (not three) outer spines on the third exopodal segment of leg 4 (armature formula II, I, 4), as follows: *S. cinctiger* Humes, 1987, *S. lomonosovi* Ivanenko and Martinez Arbizu 2006, *S. mucroniferus* Humes, 1987, *S. rimivagus* Humes, 1997, *S. serratus* Humes, 1996, *S. teres* Humes, 1996, and *S. verruculatus* Humes, 1987. In six of these species, at least one of legs 1–4 has an inner seta on the coxa. In *S. verruculatus*, the remaining species, there is no inner seta on the coxa of any of legs 1–4, which is comparable with *S. spinifer* n. sp.

Stygiopontius verruculatus, known from the East Pacific Rise, was described based only on the male (Humes 1987). Although a direct comparison between it and *S. spinifer* n. sp. may be difficult, some sexually non-dimorphic characters may be used to compare male *S. verruculatus* and female *S. spinifer* n. sp., as follows: (1) the epimeral regions of the fourth pedigerous somite are rounded in *S. spinifer* n. sp. but tapering and pointed in *S. verruculatus*; (2) the innermost distal seta on the caudal ramus of *S. spinifer* n. sp. is unilaterally pinnate, whereas that of *S. verruculatus* is naked; and (3) the inner element on the basis of the maxilliped is a seta located at the proximal third in *S. spinifer* n. sp. but a ball-like process located near distal third in *S. verruculatus*.

Stygiopontius horridus n. sp.

(Figs 13–16)

<http://zoobank.org/C29CE293-4E24-4182-A215-D555443CA734>

Material examined. Twenty three females, eight males, and one copepodid I in amplexus with a male adult, from washings of invertebrates at GTV1702 (19°33.387'S, 65°50.893'E, depth 2507 m), the Solitaire vent field on the Central Indian Ridge in the Indian Ocean, 01 August 2017. Holotype (female, MABIK CR00244731) and paratypes (20 females and seven males, MABIK CR00244732) have been deposited in the Marine Biodiversity Institute of Korea (MABIK), Seocheon. Dissected paratypes (two females and one male) are retained in the collection of the junior author.

Additional material examined. Seven females and two males from washings of invertebrates, at GTV1807 (19°33.395'S, 65°50.889'E, depth 2634 m), the Solitaire vent field, 20 June 2018.

Female. Body (Fig. 13A) moderately broad and 1.24 mm long. Prosome 710 × 545 µm. Cephalothorax 445 µm long, with angular posterolateral corners. Three metasomites with rounded posterolateral corners. Urosome (Fig. 13B) 5-segmented. Fifth pedigerous somite 149 µm wide; lateral apices not pointed. Genital double-somite 190 × 163 µm, distinctly longer than wide, with slightly expanded anterior two-fifths; genital aperture located dorsolaterally at 30% region of double-somite length. Three free abdominal somites 73 × 104, 49 × 99, and 46 × 98 µm, respectively, smooth without spinules or setules on all surfaces. Caudal rami (Fig. 13C) stout and slightly convergent; each ramus 72 × 42 µm, 1.71 times as long as wide, with tapering posteroventral margin and six naked setae; innermost distal seta as long as outermost distal seta. Egg sac (Fig. 13D) containing two or three eggs; each egg about 195 µm in diameter.

Rostrum absent. Antennule (Fig. 13E) relatively short, 273 µm long, and 10-segmented; third segment short and incompletely articulated from second segment; first segment the longest; armature formula 15, 8, 2, 4, 2, 2, 2, 2 + aesthetasc, and 13; setae naked and mostly short. Antenna (Fig. 13F) massive. Articulation between coxa and basis incomplete. Exopod small, 10 × 6 µm, with three setae. First endopodal segment unarmed but with large tubercle on inner side. Second endopodal segment (Fig. 13G) 31 × 21 µm, with two blunt spiniform setae (one on inner margin and the other on distal margin) and two robust spines tipped with bundle of spinules.

Oral cone short, stout. Mandible (Fig. 13H) with more than ten teeth distally and hyaline lamella subdistally. Maxillule (Fig. 13I) with both lobes bearing nearly parallel lateral margins; inner lobe with three setae; outer lobe subequal in length to inner lobe, with three setae; setae of outer lobe distinctly longer than those of inner lobe. Maxilla (Fig. 13J) with broad, unarmed syncoxa; basis hook-like, with fine spinules near middle; seta arising between segments naked and much shorter than basis. Maxilliped (Fig. 13K) 4-segmented; seta on syncoxa and basis small; endopod 2-segmented, but proximal segment subdivided by rudimentary articulation; proximal segment with two small setae; distal segment about 28 µm long, distally with one large seta; terminal claw 93 µm long, smooth, with denticle subdistally.

Legs 1–3 (Fig. 14A–C) with 3-segmented rami. Leg 4 (Fig. 14D) with 3-segmented exopod and 2-segmented endopod. All of these legs lacking inner coxal seta. Basis of leg 1 with mammillary process (indicated by arrowhead in Fig. 14A) at inner distal corner and thin, needle-shaped seta near base of endopod. Leg 4 with first exopodal segment bearing almost naked inner seta; third exopodal segment armed with three spines and four setae; first endopodal segment small, 26 × 23 µm; second endopodal segment 87 × 37 µm, much broader than first segment, with slightly undulating outer margin and terminal spine of 63 µm long. Armature formula of legs 1–4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1:	0-0	1-1	I-1; I-1; III, 2, 2	0-1; 0-2; 1, 2, 3
Leg 2:	0-0	1-0	I-1; I-1; III, I, 4	0-1; 0-2; 1, 2, 3
Leg 3:	0-0	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 1, I, 3
Leg 4:	0-0	1-0	I-1; I-1; II, I, 4	0-0; 0, I, 1

Leg 5 (Fig. 14E) 1-segmented, clearly articulated from somite, 77 × 54 µm, 1.43 times as long as wide, with four naked setae, innermost one of them thin. Leg 6 not seen in genital aperture (Fig. 13B).

Male. Body (Fig. 15A) markedly smaller than that of female, 776 µm long. Prosome 465 × 375 µm. Cephalothorax 306 µm long, frontally truncate. Urosome (Fig. 15B) 6-segmented. Fifth pedigerous somite 95 µm wide, with angular lateral apices. Genital somite 79 × 138 µm, much wider than long, with rounded corners. Four abdominal somites 50 × 98, 45 × 86, 28 × 72, and 33 × 72 µm, respectively, with convex lateral margins. Anal somite with several minute spinules on ventral surface near base of caudal rami (Fig. 15C). Caudal ramus (Fig. 15C) 50 × 30 µm, 1.67 times as long as wide; ventrodistal apex bilobed.

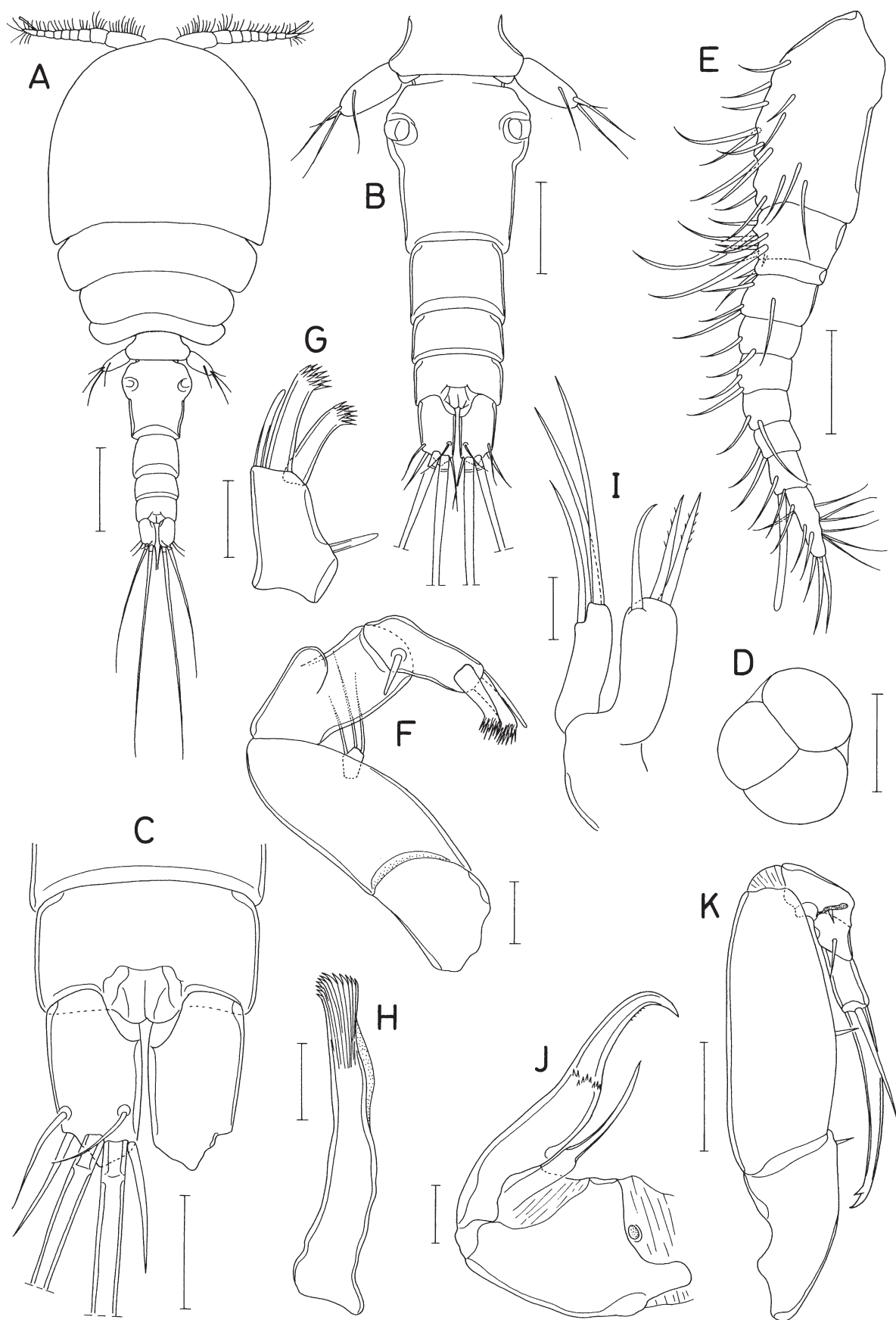


FIG. 13. *Stygiopontius horridus* n. sp., female. A, habitus, dorsal; B, urosome, dorsal; C, anal somite and caudal rami, dorsal; D, egg sac; E, antennule; F, antenna; G, terminal segment of antenna; H, mandible; I, maxillule; J, maxilla; K, maxilliped. Scale bars: A, D = 0.2 mm; B = 0.1 mm; C, E, K = 0.05 mm; F–J = 0.02 mm.

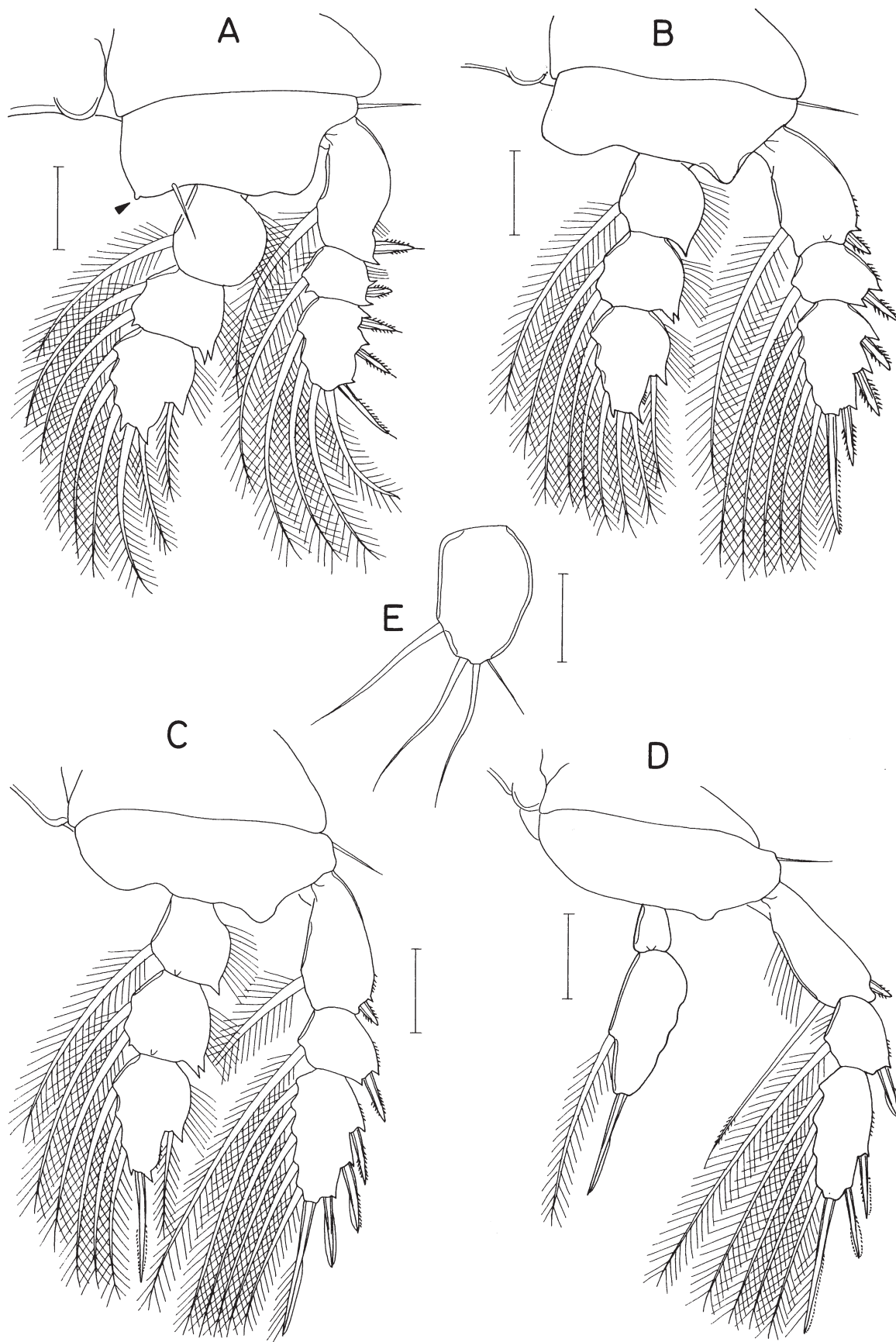


FIG. 14. *Stygiopontius horridus* n. sp., female. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5. Scale bars: 0.05 mm.

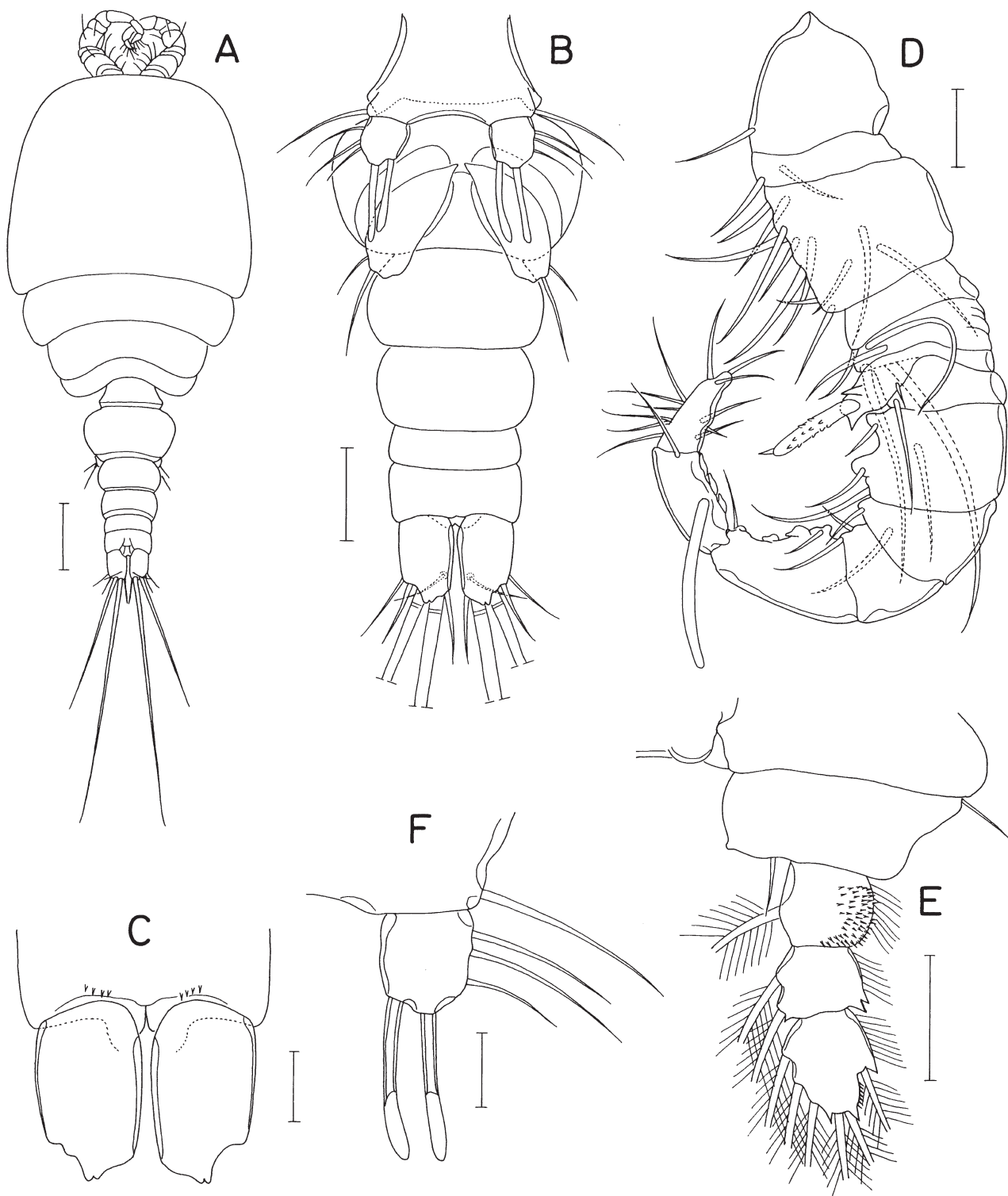


FIG. 15. *Stygiopontius horridus* n. sp., male. A, habitus, dorsal; B, urosome, ventral; C, caudal rami, ventral; D, antennule; E, coxa, basis and endopod of leg 1; F, leg 5. Scale bars: A = 0.1 mm; B, E = 0.05 mm; C, D, F = 0.02 mm.

Rostrum absent. Antennule (Fig. 15D) stout, strongly recurved, and 13-segmented; armature formula 1, 2, 12, 1, 4, spine+1, 1, 4, 2, 2, 2, 1+aesthetasc, and 12; fifth segment with about three vestiges of articulations on posterior side; sixth segment with outgrowth bearing two spiniform processes, its terminal spine with small warts on all surfaces and tipped with short seta; eighth segment with two blunt processes on anterior margin, each tipped with seta; eleventh and twelfth segments respectively with two and three distally-directed processes on anterior margin. Antenna as in female.

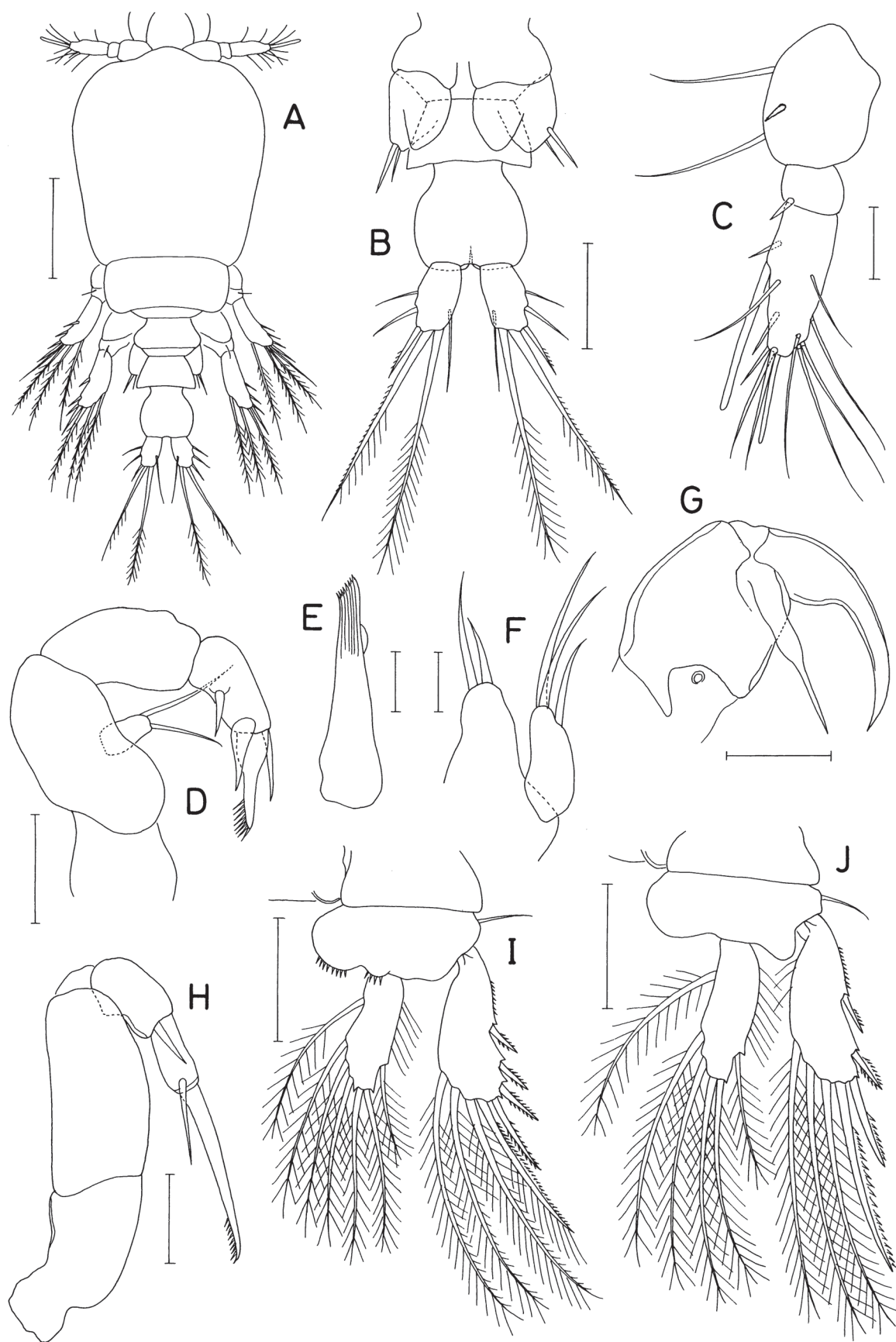


FIG. 16. *Stygiopontius horridus* n. sp., copepodid I. A, habitus, dorsal; B, urosome, ventral; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, maxilliped; I, leg 1; J, leg 2. Scale bars: A = 0.1 mm; B, I, J = 0.05 mm; C, D, G, H = 0.02 mm; E, F = 0.01 mm.

Oral cone, mandible, maxillule, maxilla, and maxilliped as female.

Leg 1 with first endopodal segment covered with numerous spinules on outer surface (Fig. 15E). Legs 2–4 as in female.

Leg 5 (Fig. 15F) 2-segmented, but protopod short and not articulated from somite, with long outer seta; exopod $27 \times 25 \mu\text{m}$, with three setae on outer margin (middle one longer than other two) and two spiniform, blunt setae on distal margin; latter two distal setae sclerotized in proximal two-thirds and lamellate in distal third. Leg 6 represented by two unequal setae on genital operculum (Fig. 15B).

Copepodid I. Body (Fig. 16A) 5-segmented, $422 \mu\text{m}$ long. Prosoma consisting of cephalothorax and second pedigerous somite. Cephalothorax $213 \times 193 \mu\text{m}$, gradually narrowing posteriorly. Urosome (Fig. 16B) 3-segmented; first urosomite being third pedigerous somite. Second urosomite $30 \times 57 \mu\text{m}$, broadening posteriorly, with angular posterolateral corners. Anal somite $50 \times 53 \mu\text{m}$, with convex lateral margins. Caudal ramus $32 \times 20 \mu\text{m}$, with six setae; longest inner distal seta bipinnate; second longest outer distal seta pinnate along inner margin and finely spinulose along outer margin.

Rostrum absent. Antennule (Fig. 16C) 3-segmented; second segment short; armature formula 3, 1, and $11 + 2$ aesthetascs. Antenna (Fig. 16D) stout. Syncoxa and basis smooth. Exopod with two distal setae. Endopod 2-segmented; first segment unarmed; second segment with two setae and two broad, spiniform elements, one of latter with spinules at distal region.

Oral cone short. Mandible (Fig. 16E) denticulate distally, with hyaline lamella at distal three-fourths. Maxillule (Fig. 16F) bilobed; outer and inner lobes with three and two setae, respectively. Maxilla (Fig. 16G) basically as in adult. Maxilliped (Fig. 16H) 4-segmented; syncoxa and basis unarmed; first and second endopodal segments each with one seta; terminal claw with spinules at distal region.

Leg 1 (Fig. 16I) and leg 2 (Fig. 16J) biramous, both rami 1-segmented and lacking inner coxal seta. Basis of leg 1 with spinules along inner distal margin. Armature formula of these two legs as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1:	0-0	1-0	IV, I, 3	1, 2, 4
Leg 2:	0-0	1-0	III, I, 3	1, 2, 3

Leg 3 (Fig. 16B) bilobed; outer lobe (exopod) with two setae; inner lobe unarmed. Legs 3–6 absent.

Etymology. The specific name *horridus*, from Latin *horrid* (prickly), alludes to the prickly tip of the distal spines of the antenna.

Remarks. *Stygiopontius horridus* n. sp. possesses the characteristic antenna and maxillule, typifying the new species. The antenna has a large tubercle on the first endopodal segment and two spinule-tipped distal spines on the second endopodal segment. The maxillule has only three (not four) setae on the inner lobe. Because these features are not shared by its congeners, the new species is easily distinguishable from other species in the genus.

Ivanenko (1998) recorded copepodid I of a dirivultid copepod found in plankton over a hydrothermal vent on the Mid-Atlantic Ridge. This copepodid I appears to be different from our specimen from the Indian Ocean mainly in body length (0.37 mm in Ivanenko's specimens), antennular segmentation (4-segmented in Ivanenko's specimens) and setation, and the morphological features of the antenna (three setae on the exopod and an elongate terminal spine on the second endopodal segment in Ivanenko's specimens).

The discovery of a copepodid I juvenile in amplexus with a male adult in the vent community implies that copepodid I of this species stays on the bottom of the vent field and that mate guarding may take place as early as the female copepodid I stage.

Stygiopontius geminus n. sp.

(Figs 17–19)

<http://zoobank.org/76F9CD5C-BB8F-4818-B658-65D745145164>

Material examined. Sixteen females and five males from sediments at GTV1701 ($19^{\circ}33.398'S$, $65^{\circ}50.899'E$,

depth 2540 m), the Solitaire vent field in the Indian Ocean, 31 July 2017. Holotype (female, MABIK CR00244733) and paratypes (11 females and three males, MABIK CR00244733) have been deposited in the Marine Biodiversity Institute of Korea (MABIK), Seocheon. Dissected paratypes (two females and one male) are retained in the collection of the junior author.

Female. Body (Fig. 17A) dorsoventrally flattened and moderately broad. Length 1.18 mm. Prosome 772 × 533 µm. Cephalothorax 413 µm long, with angular posterolateral corners in dorsal view. Three metasomal somites with blunt or rounded posterolateral corners. Urosome (Fig. 17B) 5-segmented. Fifth pedigerous somite 164 µm wide, with angular lateral apices and straight posterodorsal margin. Genital double-somite 162 × 158 µm, slightly longer than wide, with roundly expanded anterior third and pointed denticle at posterolateral corners; genital aperture located dorsolaterally at 37% region of double-somite length. Three free abdominal somites, 66 × 107, 41 × 91, and 42 × 95 µm, respectively. Caudal rami (Fig. 17C) directed backwards, 67 × 40 µm measured in ventral view, 1.68 times as long as wide, with bilobed posteroventral margin bearing spinules, transverse row of several spinules on ventral surface near posteroventral margin, and armed with six setae; two mid-terminal setae pinnate along their distal two-thirds; innermost distal seta pinnate along inner margin.

Rostrum absent. Antennule (Fig. 17D) 373 µm long and 12-segmented; armature formula 1, 14, 10, 2, 4, 2, 2, 2, 2, 2 + aesthetasc, 6, and 7 + aesthetasc; third segment with trace of articulation subdistally; aesthetasc on antepenultimate segment constricted near middle; aesthetasc on terminal segment very small. Antenna (Fig. 17E) with short, unarmed syncoxa. Basis with setules on inner margin and several spinules on outer margin near base of exopod. Exopod small, 12 × 6 µm, with three setae. Endopod 2-segmented; first segment unarmed but with row of spinules on outer side; second segment 29 × 16 µm, with two spines (108 and 58 µm long, respectively), two setae, and three groups of minute setules.

Oral cone stout and short as in other species in the genus. Mandible (Fig. 17F) with about ten teeth distally and three transparent lamellae on inner margin, distal two of latters finely pectinate and proximal one short and smooth. Maxillule (Fig. 17G) bilobed; shorter outer lobe with three large and one small setae; inner lobe with four large and one minute setae distally and setules on inner margin. Maxilla (Fig. 17H) consisting of syncoxa, basis, and intermediate seta; syncoxa with short, flexible tube at base; basis with spatulate tip bearing spinules and setules and with transverse row of spinules in middle; intermediate seta inserted on fleshy expansion arising between syncoxa and basis, articulated at base, nearly as long as basis, and pinnate distally. Maxilliped (Fig. 17I) 5-segmented; inner setae on syncoxa and basis 49 and 28 µm long, respectively; endopod with two, one, and one setae on first to third segments, respectively; third endopodal segment 22 µm long; terminal claw elongate, 125 µm long, more than five times as long as third endopodal segment, with fine spinules along inner margin.

Legs 1–3 (Fig. 18A–C) with 3-segmented rami. Leg 4 (Fig. 18D) with 3-segmented exopod and 2-segmented endopod. Inner coxal seta present in legs 1 and 2 but absent in legs 3 and 4. Inner distal seta on basis of leg 1 needle-like. Second endopodal segment of legs 1–3 with bicuspid outer distal corner. Basis of leg 2 with five or six spinules on anterior surface near inner distal corner. First segment of leg 4 endopod 29 × 20 µm; second segment 56 × 28 µm, with setules on outer margin, its terminal spine setiform and 75 µm long. Armature formula of legs 1–4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1:	0-1	1-1	I-1; I-1; III, 2, 2	0-1; 0-2; 1, 2, 3
Leg 2:	0-1	1-0	I-1; I-1; III, I, 4	0-1; 0-2; 1, 2, 3
Leg 3:	0-0	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 1, I, 3
Leg 4:	0-0	1-0	I-1; I-1; II, I, 4	0-0; 0, I, 1

Leg 5 (Fig. 18E) obscurely 2-segmented; articulation represented by transverse unsclerotized area. Proximal segment (protopod) 37 × 32 µm, its outer seta 116 µm long. Distal segment (exopod) narrowing distally, 27 × 22 µm, with three setae, longest one 96 µm long. Leg 6 (Fig. 17F) represented by 1 pinnate seta in genital aperture.

Male. Body (Fig. 19A) 903 µm long. Prosome relatively broad, 510 × 449 µm. Cephalothorax 315 µm long, with pointed posterolateral corners. Urosome (Fig. 19B) 6-segmented, fifth pedigerous somite 108 µm wide. Genital somite wider than long, 93 × 136 µm, with rounded corners; genital operculum (Fig. 19H) with spinules on inner and outer sides. Four abdominal somites 80 × 97, 58 × 87, 33 × 78, and 29 × 76 µm, respectively; first abdominal somite with pointed denticle at posterolateral corners. Anal somite shortest among abdominal somites, with spinules near posteroventral margin (Fig. 19C). Caudal ramus (Fig. 19C) 52 × 33 µm, 1.58 times as long as wide.

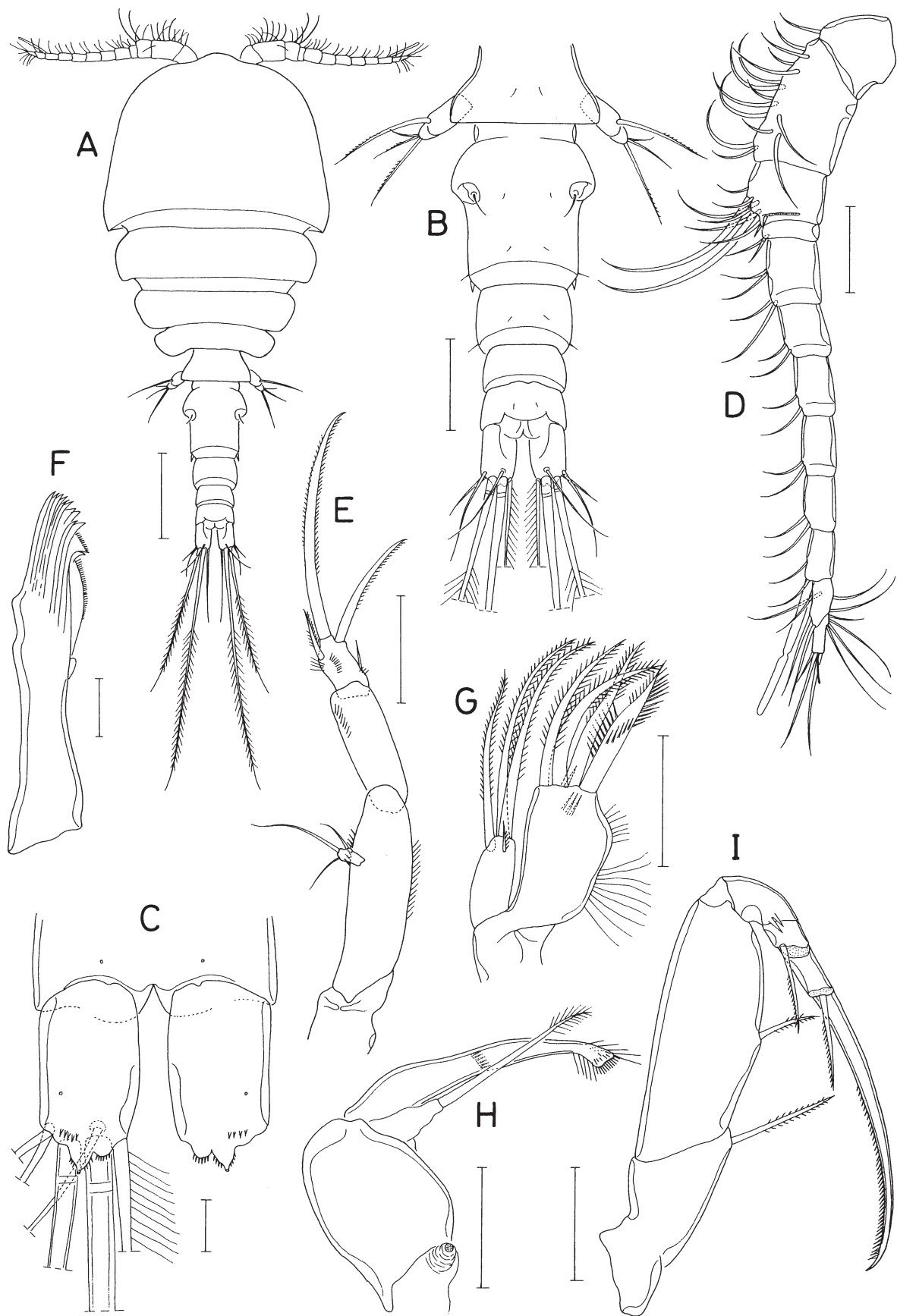


FIG. 17. *Stygiopontius geminus* n. sp., female. A, habitus, dorsal; B, urosome, dorsal; C, caudal rami, ventral; D, antennule; E, antenna; F, mandible; G, maxillule; H, maxilla; I, maxilliped. Scale bars: A = 0.2 mm; B = 0.1 mm; C, F = 0.02 mm; D, E, G–I = 0.05 mm.

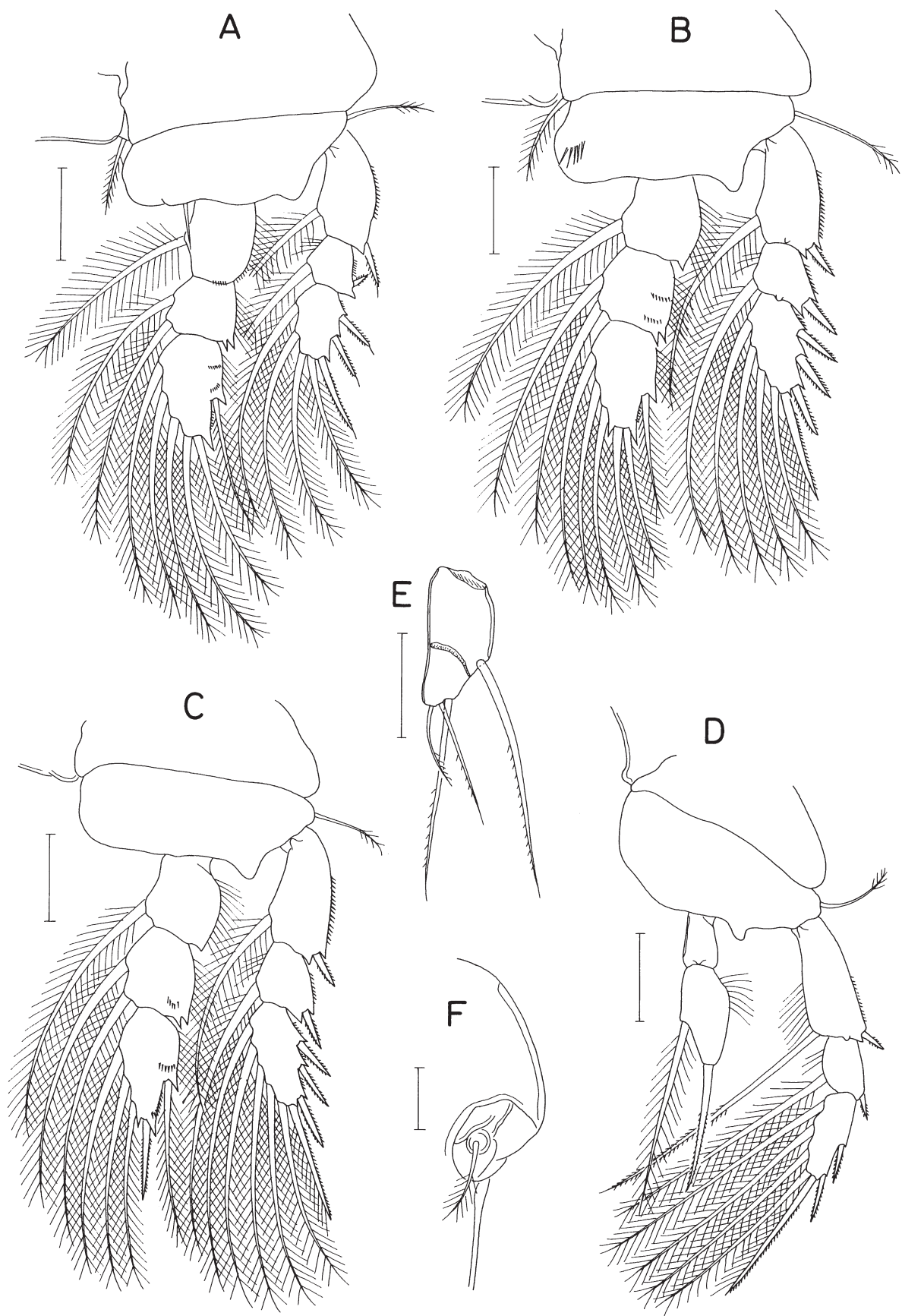


FIG. 18. *Stygiopontius geminus* n. sp., female. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5; F, right genital aperture. Scale bars: A–E = 0.05 mm; F = 0.02 mm.

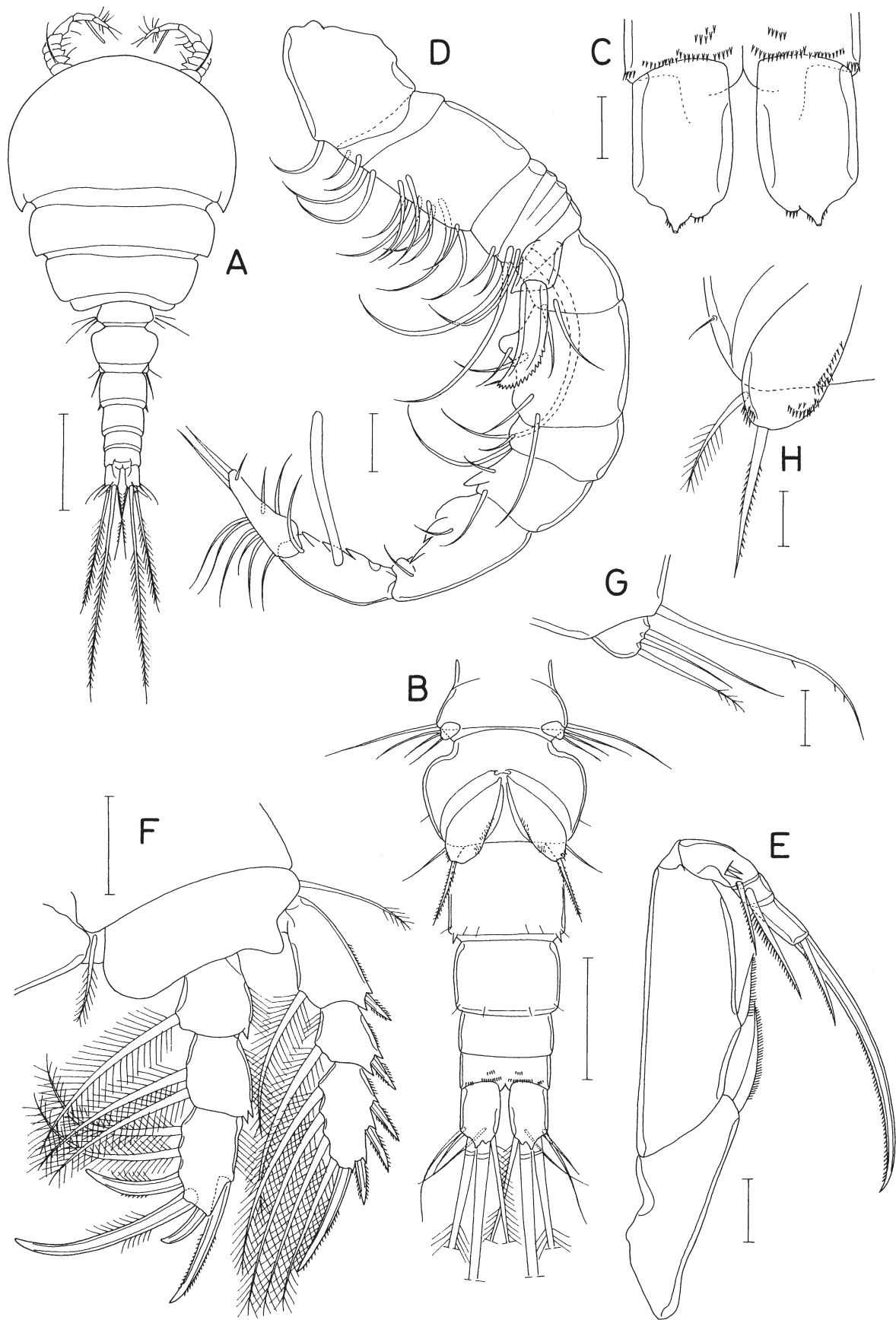


FIG. 19. *Stygiopontius geminus* n. sp., male. A, habitus, dorsal; B, urosome, ventral; C, caudal rami, ventral; D, antennule; E, maxilliped; F, leg 2; G, leg 5; H, leg 6. Scale bars: A = 0.2 mm; B = 0.1 mm; C–E, G, H = 0.02 mm; F = 0.05 mm.

Rostrum absent. Antennule (Fig. 19D) strongly curved and 13-segmented; armature formula 1, 2, 12, 2, 4, spine, 2, 4, 2, 2, 2, 1 + aesthetasc, and 11; spine on sixth segment inserted on outgrowth of segment, strong, serrate on distal margin, and tipped with one small setule; eighth segment with round protrusion on anterior margin; tenth to twelfth segments with one, two, and three spiniform processes, respectively, on anterior margin. Antenna as in female.

Oral cone, mandible, maxillule, and maxilla as in female. Maxilliped (Fig. 19E) 5-segmented; inner seta on syncoxa and basis expanded, spinulose along inner (posterior) margin, and 34 and 22 μm long, respectively. Outer margin of basis smooth. Endopod with three, one, and one setae on first to third segments, respectively.

Leg 1 as in female. Leg 2 (Fig. 19F) with third endopodal segment bearing four strong spines and two setae; lengths of these spines 70, 25, 100, and 44 μm , from outer to inner. Legs 3 and 4 as in female.

Leg 5 (Fig. 19G) with protopod fused with somite, with long outer seta. Exopod small, 13 \times 21 μm , with three setae on outer margin. Leg 6 (Fig. 19H) represented by two setae on genital operculum.

Etymology. The specific name *geminus* is derived from the Latin *gemin* (=twin), referring to the close similarity of the new species to *Stygiopontius lomonosovi* Ivanenko and Martinez Arbizu, 2006 in Ivanenko, Martinez Arbizu and Stecher (2006).

Remarks. As diagnostic features of *S. geminus* n. sp., the third exopodal segment of leg 4 has three spines and four setae (armature formula II, I, 4) and the inner coxal seta present in legs 1 and 2. This feature is shared by three known species: *S. cinctiger* Humes, 1987, *S. teres* Humes, 1996, and *S. lomonosovi* Ivanenko and Martinez Arbizu, 2006. *Stygiopontius cinctiger* has a broad, ventrally swollen genital double-somite in the female and is, therefore, easily distinguishable from the other three species. *Stygiopontius teres* differs also in the female from those of *S. lomonosovi* and *S. geminus* n. sp. in having an oviform prosome, tapering epimeral regions of the fourth pedigerous somite, unsegmented broad leg 5, and all bipinnate caudal setae. Females of the remaining two species, *S. lomonosovi* and *S. geminus* n. sp., are hardly distinguishable, except for a slight difference in the dimensions of the caudal ramus. The length-to-width ratio of the caudal ramus in the female *S. lomonosovi* is at most 1.45 based on the original illustration (Fig. 5E of Ivanenko *et al.* 2006), compared with 1.68 in *S. geminus* n. sp.

However, because males of the two species differ markedly, they cannot be treated as conspecific. For example, the inner distal corner of the maxilliped syncoxa of the male is strongly projected in *S. lomonosovi* but not projected in *A. geminus* n. sp., and a prominent outgrowth on the third antennular segment in the male described and illustrated in *S. lomonosovi* (see Ivanenko *et al.* 2006) is absent in the male of *S. geminus* n. sp. These and other differences are summarized in Table 1.

TABLE 1. Differences between *Stygiopontius lomonosovi* Ivanenko & Martinez Arbizu, 2006 and *S. geminus* n. sp.

Characters	<i>S. lomonosovi</i>	<i>S. geminus</i> n. sp.
Body length ♀	0.93 mm	1.18 mm
♂	1.03 mm	0.90 mm
Caudal ramus, L/W ♀	1.45:1*	1.68:1
♂	1.40:1*	1.58:1
Outer margin of maxilliped basis	With spinules	Smooth
Inner distal corner of syncoxa of ♂ maxilliped	Strongly projected	Not projected
Inner setae on syncoxa and basis of ♂ maxilliped	Slender	Broad
Third segment of ♂ antennule	With a prominent outgrowth	Without an outgrowth
Outer spine on third endopodal segment of ♂ leg 2	Small, much shorter than segment	Large, much longer than segment
Distribution	Mid-Atlantic Ridge	Central Indian Ridge

*Length/width ratios of caudal rami of *S. lomonosovi* were measured based on the original illustrations.

***Stygiopontius quadripaxillifer* n. sp.**

(Figs 20–22)

<http://zoobank.org/2CF78CF5-28FB-453F-B062-F9C501E55D3F>

Material examined. One female (holotype, MABIK CR00244735) and one male (paratype, MABIK CR00244736) from sediments at GTV1701 (19°33.398'S, 65°50.899'E, depth 2540 m), the Solitaire vent field in the Indian Ocean, 31 July 2017. All specimens have been dissected and mounted on the slide, and deposited in the Marine Biodiversity Institute of Korea (MABIK), Seocheon.

Female. Body (Fig. 20A) moderately narrow and dorsoventrally flattened. Length 1.08 mm. Prosome 612 × 447 µm. Cephalothorax 340 µm long, with pointed posterolateral corners. Second to fourth pedigerous somites with rounded posterolateral corners. Urosome (Fig. 20B) 5-segmented. Fifth pedigerous somite 165 µm wide, laterally tapering, with pointed lateral apices. Genital double-somite 142 × 155 µm; anterior third slightly expanded with pointed claw-like process on both sides at level of genital apertures (Fig. 21F); posterior two-thirds 131 µm wide, with slightly convex lateral margins and angular posterolateral corners; genital aperture located dorsolaterally. Three free abdominal somites 80 × 116, 54 × 97, and 43 × 84 µm, respectively. First free abdominal somite with convex lateral margins and angular posterolateral corners. Anal somite shorter than preceding somite, with several spinules on posteroventral surface (Fig. 20C). Caudal rami (Fig. 20C) directed straightly backwards, 82 × 35 µm, 2.34 times as long as wide, with six naked setae, and several spinules on ventrodistal surface; posteroventral margin with short tube bearing pore at tip; innermost distal seta characteristically inflated proximally.

Rostrum absent. Antennule (Fig. 20D) 304 µm long and 13-segmented; articulation between last two segments faint; third segment longest; armature formula 1, 2, 12, 9, 2, 4, 2, 2, 2, 2 + aesthetasc, 6, and 7; first segment with several setules on anterior margin; aesthetasc on penultimate segment constricted in middle. Antenna (Fig. 20E) with unarmed, short syncoxa; basis with several spinules on outer and inner margins. Exopod small, 10 × 6 µm, with three setae. First endopodal segment unarmed, with few minute spinules on inner margin. Second endopodal segment 28 × 16 µm, with two spines (83 and 49 µm, respectively), two setae, and three groups of setules.

Oral cone stout. Mandible (Fig. 20F) and maxilla (Fig. 20H) similar to those of *S. geminus* n. sp. Maxillule (Fig. 20G) bilobed; outer lobe small, half as long as inner lobe with three large and one minute setae; inner lobe with four large and one minute setae and with few spinules subdistally and setules on inner margin. Maxilliped (Fig. 20I) 5-segmented; inner distal seta on syncoxa 40 µm long; basis with few spinules on outer margin, seta on inner margin 34 µm long; three endopodal segments with three, one, and one setae, respectively; three setae on first endopodal segment small; terminal claw 97 µm long, slightly arched, spinulose along inner margin, about four times as long as third endopodal segment (24 µm long).

Legs 1–4 (Fig. 21A–D) lacking coxal seta. Leg 1 basis with patch of spinules near inner distal corner. Inner distal region of leg 2 basis protruded, with six or seven spinules on its anterior surface (Fig. 21B). Leg 4 endopodal segments 29 × 20, and 57 × 26 µm, respectively; terminal spine on second endopodal segment setiform and 68 µm long. Armature formula of legs 1–4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1:	0-0	1-1	I-1; I-1; III, 2, 2	0-1; 0-1; 1, 2, 3
Leg 2:	0-0	1-0	I-1; I-1; III, I, 4	0-1; 0-2; 1, 2, 3
Leg 3:	0-0	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 1, I, 3
Leg 4:	0-0	1-0	I-1; I-1; III, I, 4	0-0; 0, I, 1

Leg 5 (Fig. 21E) 2-segmented; segmentation represented by transverse unsclerotized band; proximal segment (protopod) about 24 × 19 µm, with large outer seta of 92 µm long; distal segment (exopod) 34 × 13 µm, about 2.6 times as long as wide, with three setae, largest proximal one of latter 84 µm long. Leg 6 (Fig. 21F) represented by one naked seta in genital aperture.

Male. Body (Fig. 22A) similar to that of female. Length 718 µm. Prosome 417 × 298 µm. Cephalothorax with four peg-like spinules on each anterolateral margin (Fig. 22B); these four spinules simple, about 9 µm long, not bifurcate at tip. Urosome 6-segmented. Fifth pedigerous somite narrow, 73 µm wide. Genital somite much wider

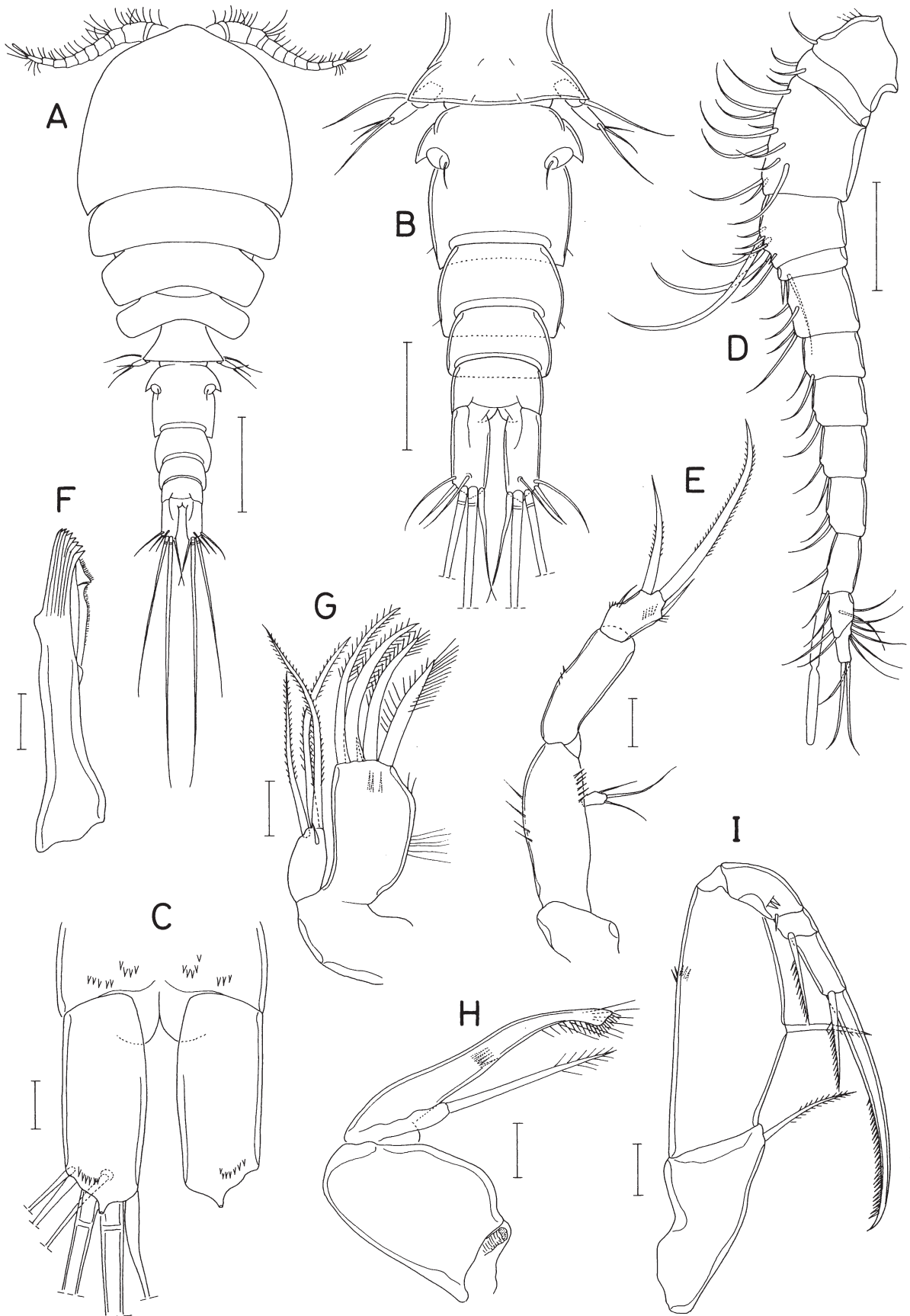


FIG. 20. *Stygiopontius quadripaxillifer* n. sp., female. A, habitus, dorsal; B, urosome, dorsal; C, caudal rami, ventral; D, antennule; E, antenna; F, mandible; G, maxillule; H, maxilla; I, maxilliped. Scale bars: A = 0.2 mm; B = 0.1 mm; C, E–I = 0.02 mm; D = 0.05 mm.

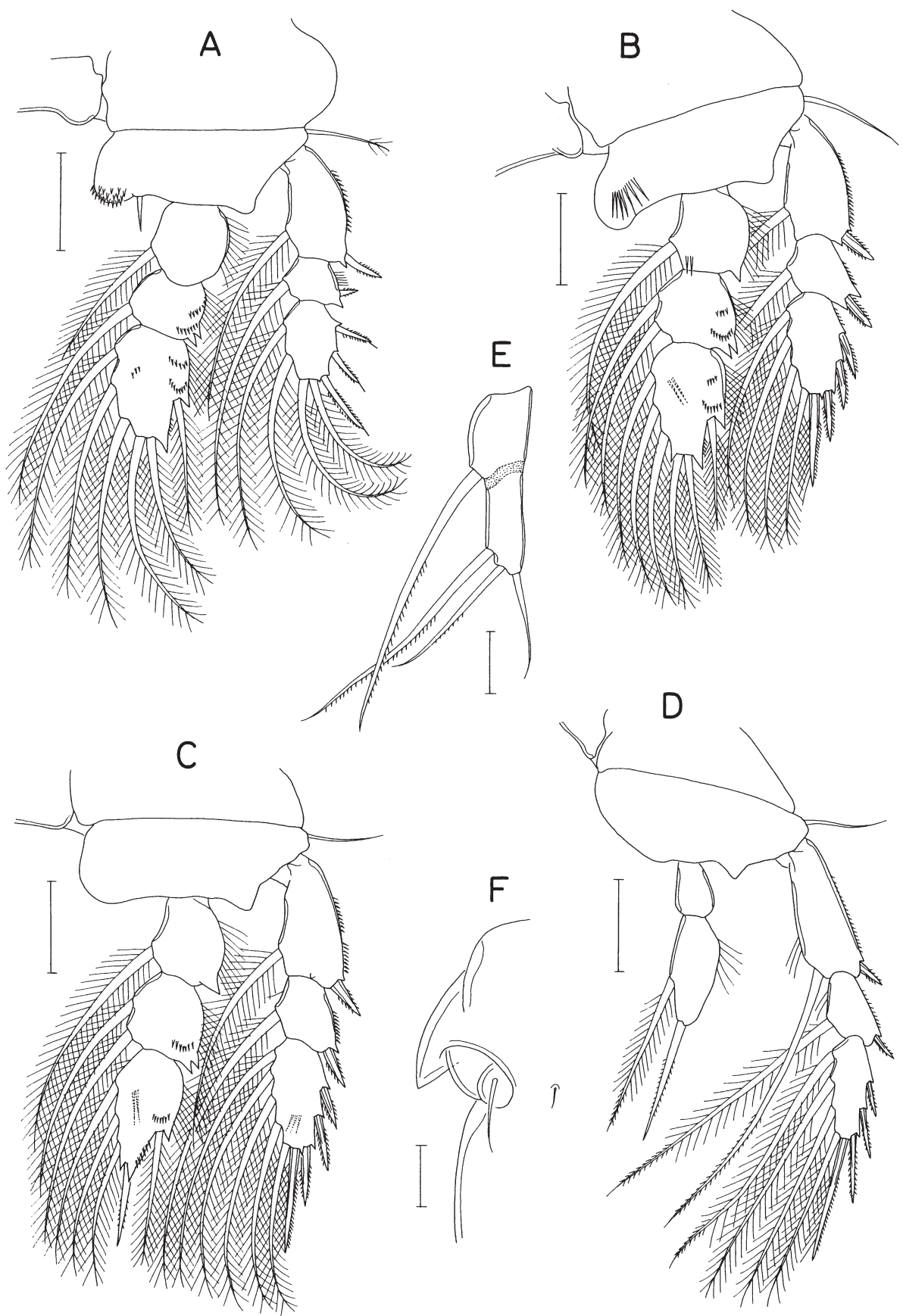


FIG. 21. *Stygiopontius quadripaxillifer* n. sp., female. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5; F, left genital aperture. Scale bars: A–D = 0.05 mm; E, F = 0.02 mm.

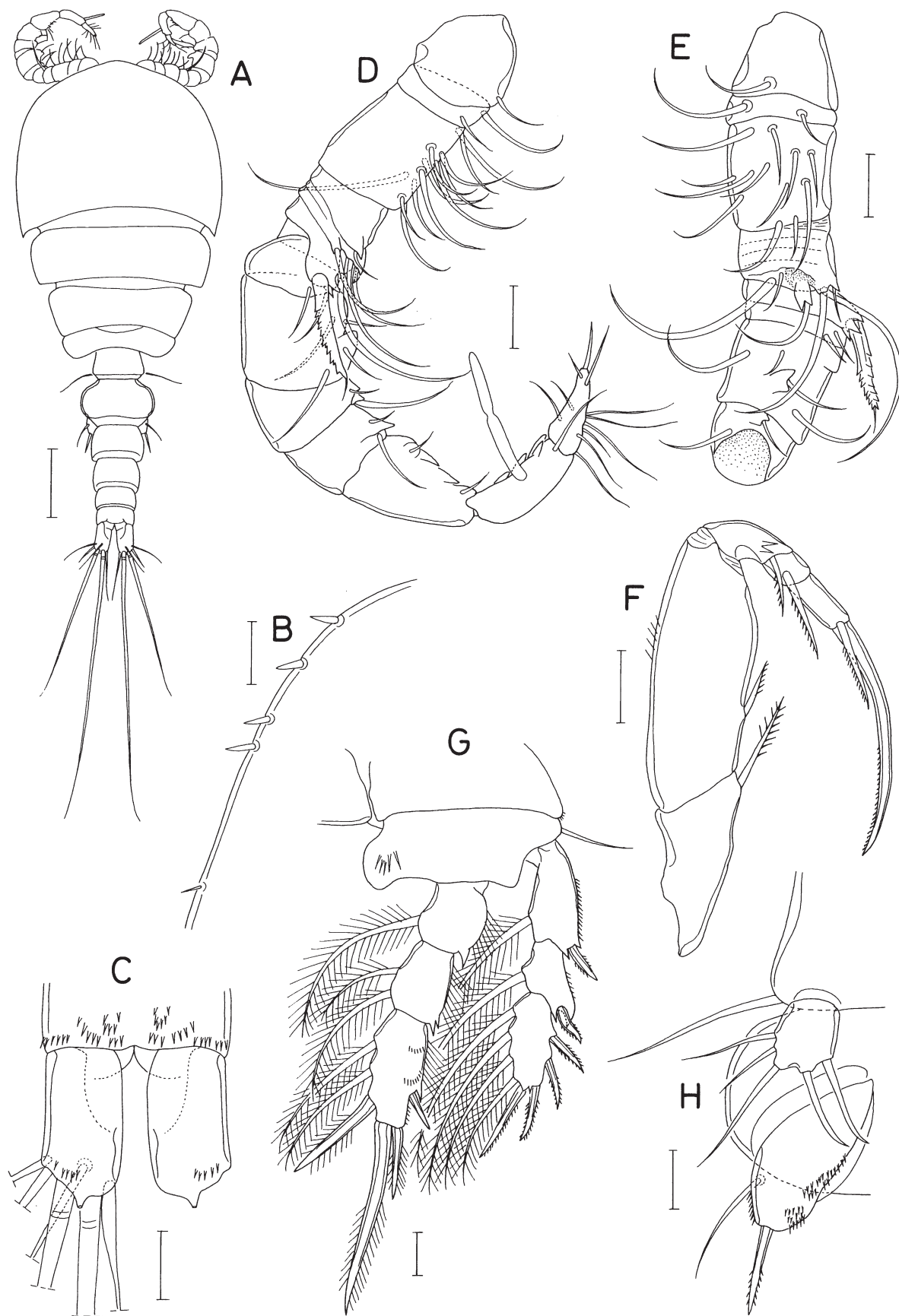


FIG. 22. *Stygiopontius quadripaxillifer* n. sp., male. A, habitus, dorsal; B, anterior part of left lateral margin of cephalothorax, dorsal; C, caudal rami, ventral; D, antennule; E, first to eighth segments of antennule, medial; F, maxilliped; G, leg 2; H, right legs 5 and 6, ventral. Scale bars: A = 0.1 mm; B–H = 0.02 mm.

than long, $71 \times 104 \mu\text{m}$, with convex lateral margins; genital operculum with three groups of spinules (one lateral and two medial). Four abdominal somites 50×74 , 47×69 , 32×58 , and $24 \times 54 \mu\text{m}$, respectively. Anal somite with more spinules on ventrodiscal surface than in female (Fig. 22C). Caudal ramus (Fig. 22C) shorter than that of female, $43 \times 23 \mu\text{m}$, 1.87 times as long as wide.

Rostrum absent. Antennule (Fig. 22D, E) 12-segmented; armature formula 1, 2, 12, 6, spine, 2, 4, 2, 2, 2, 1+aesthetasc, and 11; fourth segment with three transverse articulation vestiges, with small process bearing bifurcate tip and a seta. Similar process present on seventh to ninth segments; spine of fifth segment denticulate in two rows and tipped with setule. Antenna as in female.

Oral cone, mandible, maxillule, maxilla as in female. Maxilliped (Fig. 22F) as in female, but distal seta on first endopodal segment larger than that of female.

Leg 1, 3 and 4 as in female. Leg 2 (Fig. 22G) with second exopodal segment bearing inflated, inwardly curved outer process on outer margin; third endopodal segment with four spines (armature formula I, II, I+2), 17, 34, 93, and $50 \mu\text{m}$ long, respectively, from outer to inner.

Leg 5 (Fig. 22H) consisting of naked outer seta on fifth pedigerous somite and free exopod. Exopod slightly longer than wide, with five naked setae (three on outer margin and two on distal margin). Leg 6 (Fig. 22H) consisting of outer seta and weakly spinulose distal spine on genital operculum.

Etymology. The specific name *quadripaxillifer* is derived from Latin *quadr* (=four), *paxillus* (=a peg) and *fero* (=to bear), alluding to the presence of the four peg-like spinules on each side of the cephalothorax in the male.

Remarks. *Stygiopontius quadripaxillifer* n. sp. has, as diagnostic features, a patch of spinules on the inner distal region of the basis of leg 1 in both sexes and peg-like spinules on the anterolateral margin of the cephalothorax in the male. One or both of these features are shared by four congeners: *S. appositus* Humes, 1989, *S. hispidulus* Humes, 1987, *S. paxillifer* Humes, 1989, and *S. sentifer* Humes, 1987, all of which known from the East Pacific Rise (Humes 1987, 1989). *Stygiopontius hispidulus* and *S. sentifer* lack an inner seta on the coxa of legs 1 and 2, and are, therefore, not necessary to compare further with the new species. The remaining two species, *S. appositus* and *S. paxillifer* which were known based only on the male, are differentiated from the new species by their longer caudal ramus (more than 2.3 times as long as wide in both species, in contrast to 1.87 times as long as wide in the male of *S. quadripaxillifer* n. sp.), by their exopod of male leg 5 which is much wider than long (vs. longer than wide in *S. quadripaxillifer* n. sp.), and by their uninflated innermost distal caudal seta (vs. the same seta being inflated proximally in *S. quadripaxillifer* n. sp.).

Acknowledgements

We thank the captain and crew members of the RV ISABU for help and support during the cruises. This research was supported by the project “Understanding the deep sea biosphere on seafloor Hydrothermal Vent in the Indian Ridge” of the Korea Institute of Marine Science and Technology Promotion (KIMST) funded by Ministry of Oceans and Fisheries, Korea (20170411) and by KIOST(PM61190).

References

- Copley, J.T., Marsh, L., Glover, A.G., Hühnerbach, V., Nye, V.E., Reid, W.D.K., Sweeting, C.J., Wigham, B.D. & Wiklund, H. (2016) Ecology and biogeography of megafauna and macrofauna at the first known deep-sea hydrothermal vents on the ultraslow-spreading Southwest Indian Ridge. *Scientific Reports*, 6, 1–13.
<https://doi.org/10.1038/srep39158>
- Gollner, S., Ivanenko, V.N., Arbizu, P.M. & Bright, M. (2010) Advances in taxonomy, ecology, and biogeography of Dirivultidae (Copepoda) associated with chemosynthetic environments in the deep sea. *PLoS ONE*, 5, e9801.
<https://doi.org/10.1371/journal.pone.0009801>
- Hashimoto, J., Ohta, S., Gamo, T., Chiba, H., Yamaguchi, T., Tsuchida, S., Okudaira, T., Watabe, H., Yamanaka, T. & Kitazawa, M. (2001) First hydrothermal vent communities from the Indian Ocean discovered. *Zoological Science*, 18, 717–721.
<https://doi.org/10.2108/zsj.18.717>
- Humes, A.G. (1984) *Benthoxynus spiculifer* n. gen., n. sp. (Copepoda: Siphonostomatoida) associated with Vestimentifera (Pogonophora) at a deep-water geothermal vent off the coast of Washington. *Canadian Journal of Zoology*, 62, 2594–2599.
<https://doi.org/10.1139/z84-380>

- Humes, A.G. (1987) Copepoda from deep-sea hydrothermal vents. *Bulletin of Marine Science*, 41, 645–788.
- Humes, A.G. (1988) Copepoda from deep-sea hydrothermal vents and cold seeps. *Hydrobiologia*, 167/168, 549–554.
<https://doi.org/10.1007/bf00026351>
- Humes, A.G. (1989) Copepoda from deep-sea hydrothermal vents at the East Pacific Rise. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 4e Série, 11, section A, 4, 829–848.
- Humes, A.G. (1990) Copepods (Siphonostomatoida) from a deep-sea hydrothermal vent at the Mariana Back-Arc Basin in the Pacific, including a new genus and species. *Journal of Natural History*, 24, 289–304.
<https://doi.org/10.1080/00222939000770211>
- Humes, A.G. (1996) Deep-sea Copepoda (Siphonostomatoida) from hydrothermal sites on the Mid-Atlantic Ridge at 23° and 37°. *Bulletin of Marine Science*, 58, 609–653.
- Humes, A.G. (1998). Copepoda from deep-sea hydrothermal sites and cold seeps: description of a new species of *Aphotopontius* from the East Pacific Rise and general distribution. *Cahiers de Biologie Marine*, 39, 51–62.
<https://doi.org/10.21411/CBM.A.958AE7F7>
- Humes, A.G. & Gooding, R.U. (1964) A method for studying the external anatomy of copepods. *Crustaceana*, 6, 238–240.
<https://doi.org/10.1163/156854064x00650>
- Humes, A.G. & Lutz, R.A. (1994) *Aphotopontius acanthinus*, new species (Copepoda: Siphonostomatoida), from deep-sea hydrothermal vents on the East Pacific Rise. *Journal of Crustacean Biology*, 14, 337–345.
<https://doi.org/10.2307/1548913>
- Ivanenko, V.N. (1998) Deep-sea hydrothermal vent Copepoda (Siphonostomatoida, Dirivultidae) in plankton over the Mid-Atlantic Ridge (29°N), morphology of their copepodid stage. *Zoologicheskii Zhurnal*, 77, 1249–1256. [in Russian with English summary]
- Ivanenko, V.N. & Heptner, M.V. (1998) New data on morphology and redescription of *Aphotopontius mammillatus* Humes, 1987 (Copepoda, Siphonostomatoida, Dirivultidae) from deep-sea hydrothermal vents in the eastern Pacific (Guaymas Basin). *Journal of Marine Systems*, 15, 243–254.
[https://doi.org/10.1016/s0924-7963\(97\)00067-5](https://doi.org/10.1016/s0924-7963(97)00067-5)
- Ivanenko, V.N., Martinez Arbizu, P. & Stecher, J. (2006) Copepods of the family Dirivultidae (Siphonostomatoida) from deep-sea hydrothermal vent fields on the Mid-Atlantic Ridge at 14°N and 5°S. *Zootaxa*, 1277 (1), 1–21.
<https://doi.org/10.11646/zootaxa.1277.1.1>
- Nakamura, K., Watanabe, H., Miyazaki, J., Takai, K., Kawagucci, S., Noguchi, T., Nemoto, S., Watsuji, T., Matsuzaki, T., Shibuya, T., Okamura, K., Mochizuki, M., Orihashi, Y., Ura, T., Asada, A., Daniel, M., Koonjul, M., Singh, M., Beedessee, G., Bhikajee, M. & Tamaki, K. (2012) Discovery of new hydrothermal activity and chemosynthetic fauna on the Central Indian Ridge at 18–20°S. *PLoS One*, 7, e32965.
<https://doi.org/10.1371/journal.pone.0032965>
- Schander, C., Rapp, H.T., Kongsrud, J.A., Bakken, T., Bberge, J., Cochrane, S., Oug, E., Byrkjedal, I., Todt, C., Cedhagen, T., Fosshagen, A., Gebrul, A., Larsen, K., Levin, L., Obst, M., Pleijel, F., Stöhr, S., Warén, A., Mikkelsen, T., Hadler-Jacobsen, S., Keuning, R., Petersen, K.H., Thorseth, I.H. & Pedersen, R.B. (2010) The fauna of hydrothermal vents on the Mohn Ridge (North Atlantic). *Marine Biology Research*, 6, 155–171.
<https://doi.org/10.1080/17451000903147450>
- Teixeira, S., Cambon-Bonavita, M.-A., Serrão, E.A., Daniel Desbruyères, D. & Arnaud-Haond, S. (2011) Recent population expansion and connectivity in the hydrothermal shrimp *Rimicaris exoculata* along the Mid-Atlantic Ridge. *Journal of Biogeography*, 38, 564–574.
<https://doi.org/10.1111/j.1365-2699.2010.02408.x>
- Tunnicliffe, V., McArthur, A.G. & McHugh, D. (1998) A biogeographical perspective of the deep-sea hydrothermal vent fauna. *Advances in Marine Biology*, 34, 355–442.
[https://doi.org/10.1016/s0065-2881\(08\)60213-8](https://doi.org/10.1016/s0065-2881(08)60213-8)
- Van Dover, C.L., Humphris, S.E., Fornari, D., Cavanaugh, C.M., Collier, R., Goffredi, S.K., Hashimoto, J., Lilley, M.D., Reisenbach, A.L., Shank, T.M., Von Damm Banta, K.L., Gallant, R.M., Götz, D., Green, D., Hall, J., Harmer, T.L., Hurtado, L.A., Johnson, P., McKiness, Z.P., Meredith, C., Olsen, E., Pan, I.L., Turnipseed, M., Won, Y., Young, III C.R. & Verijenhoeck, R.C. (2001) Biogeography and ecological setting of Indian Ocean hydrothermal vents. *Science*, 294, 818–823.
<https://doi.org/10.1126/science.1064574>
- Watanabe, H. & Beedessee, G. (2015) Vent fauna on the Central Indian Ridge. In: Ishibashi, J.-I., Okino, K. & Sunamura, M. (Eds.), *Subseafloor Biosphere Linked to Hydrothermal Systems, TAIGA Concept*. Springer, Japan, Tokyo, pp. 205–211.
https://doi.org/10.1007/978-4-431-54865-2_16